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An ecological study of small mammals in southeast Queensland rainforest.

by

D.H. Wood M.Sc.

Zoology Department, University of Queensland.

A thesis submitted in accordance with the requirements of the Degree of Doctor of Philosophy of the University of Queensland.

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PREFACE

The investigations described in this thesis were carried out at the Zoology Department, University of Queensland, Brisbane, during the years 1963 - 1967, under the supervision of Dr. A.K. Lee, Dr. M.C. Bleakley and Dr. J. Kikkawa.

The thesis is the original work of the author and it has not been submitted in any form at another university.

D.H. Wood.

October, 1967.

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I. INTRODUCTION

Sixty seven species of rodents have been recorded from Australia (Tate, 1951) including the three introduced species Rattus norvegicus Berkenhout, R. rattus Linne, and Mus musculus Linne. All these species belong to the Muridae, a family which has received scant attention regarding field populations in Australia.

The water rat, Hydromys chrysogaster Geoffroy has been studied by McNally (1960). He recorded body weight and length measurements, condition of male and female reproductive organs, condition of pelage, disease, parasites and body injuries, and discussed population turnover.

The broad toothed rat, Mastacomys fuscus Thomas has been studied both in its natural habitat and in captivity by Calaby and Wimbush (1964). They recorded some micro-climate data of its habitat, associated species, and breeding and weight changes of a few individuals in the laboratory.

The field rat, Rattus conatus Thomas has been thoroughly investigated both in the laboratory and the field by McDougall (1944a, 1944b, 1944c, 1946a, 1946b). Its population dynamics and movements in the field have been recorded, and its reproductive biology and growth have been closely studied both in the field and the laboratory.

The bush rat, Rattus fuscipes (Waterhouse) has been studied by Taylor (1961) and Warneke (1964). Taylor (1961) obtained data on movements, breeding, and growth from a live trapping study in eucalypt forest in

New South Wales, and made a more intensive study of breeding and growth in the laboratory. Warneke (1964) worked on R. fuscipes in exotic pine plantations in Victoria. He carried out field and laboratory work on reproduction, growth, age determination, and diet, as well as making a live trapping study of movements and population changes.

The velvet furred rat, Rattus lutreolus Thomas has recently received attention in the field and in captivity (Green, 1967). In the field its movements and breeding have been studied, and its habitat described, and, from laboratory work, growth rates and more detailed observations on breeding have been recorded.

Turning to the small "rat and mouse like" marsupials of Australia, there are some 30 species, all belonging to the family Dasyuridae. These have received even less attention in the field than the murids. There is one short paper by Horner and Taylor (1959) on Antechinus stuartii Macleay describing the pouch and pouch young, and recording some movements of a few individuals which were recaptured two or three times in the field.

No detailed studies of any members of these two families have been carried out in the Australian tropical and sub-tropical rain forests, though some trapping to determine distributions and relative abundance has been carried out in selected areas (McDougall, 1946b, Tate, 1952, Harrison, 1962a, Calaby, 1966).

The present study attempts to determine on a quantitative basis the breeding season, growth, movements, mortality, population size and structure, and habitat utilisation of the three small mammals that inhabit sub-tropical rain forest in the Brisbane area of south-east Queensland, - Rattus fuscipes and Melomys cervinipes (Gould) (Muridae), and Antechinus stuartii (Dasyuridae).

II TAXONOMY AND GENERAL HABITS OF SPECIES STUDIED

A. Rattus fuscipes (Waterhouse)

The name of this species has recently been re-examined by Horner and Taylor (1965). Ellerman (1949) grouped R. assimilis (Gould) together with two other species R. greyi (Gray) and R. fuscipes (Waterhouse) as R. fuscipes (Waterhouse), but later Tate (1951) recognised R. assimilis (Gould) and R. greyi (Gray) as two closely related species, and placed R. fuscipes (Waterhouse) as a subspecies of R. lutreolus (Gray). The biosystematic study of these four species of Rattus carried out by Horner and Taylor (1965) convincingly demonstrated conspecificity for R. fuscipes (Waterhouse), R. greyi (Gray) and R. assimilis (Gould). Horner and Taylor claim (1965, p.108) that these three species "..... are referable, by the rule of priority, to the species Rattus fuscipes (Mus fuscipes) Waterhouse, 1839)." The animals used by Horner and Taylor were captured in the field about 20 miles south-west of Canberra, and since no worker has suggested even subspecific differences in R. fuscipes (Waterhouse) over that part of its range from Gympie (about 100 miles north of Brisbane) through New South Wales to eastern Victoria, the name allotted to the species by Horner and Taylor (1965) has been used in this study.

R. fuscipes (Plate I) can be described as a typical rat of the forest floor. Adult females weigh about 130 g. and males are somewhat heavier, up to 200 g. Individuals do not appear above ground in daylight, and at night rarely leave the forest floor. They feed on fallen fruits, other vegetable matter, and insects (Harrison, 1961; Warneke, 1964).

B. Melomys cervinipes (Gould)

This species can be identified as Melomys cervinipes cervinipes (Gould) of Tate (1951), the two cotypes of which were collected on Stradbroke Island, off Brisbane. In a general statement on the species Tate (1951 p.292) notes that: "Melomys cervinipes is primarily a rain forest species."

M. cervinipes (Plate 2) is a short-nosed "plump" rat, and is smaller than R. fuscipes. Adult females weigh about 70g., males are slightly heavier, up to 100g. Individuals are only active during the hours of darkness, and can climb with agility. Their diet includes fruit, but they mainly browse on shoots and leaves. Insects are taken rarely (Harrison, 1961). This species is difficult to trap.

C. Antechinus stuartii Macleay

The specific name stuartii has not been used in the more recent literature, flavipes having been misused in its stead. Confusion of the species with A. flavipes (Waterhouse) arose, according to Wakefield and Warneke (1967 p.88), when: "Iredale and Troughton (1934) misapplied the trinomial Antechinus flavipes flavipes to the central-eastern New South Wales population which is, in fact, the nominate form of A. stuartii. This error has been perpetuated in many subsequent publications dealing with that population (Troughton, 1941; Tate, 1947; Horner and Taylor, 1959; Marlow, 1961; etc.)". The species dealt with in this study was Antechinus stuartii Macleay as redescribed by Wakefield and Warneke (1967).

A. stuartii (Plate 3) is a small shrew-like marsupial. Adult females weigh about 30g., males up to 60 or 70g. They are usually nocturnal, but activity sometimes occurs during daylight. Though scansorial in habit, individuals also forage amongst the forest floor litter for insects and invertebrates (Wakefield and Warneke, 1967).

Plate 1. Adult female Rattus fuscipes

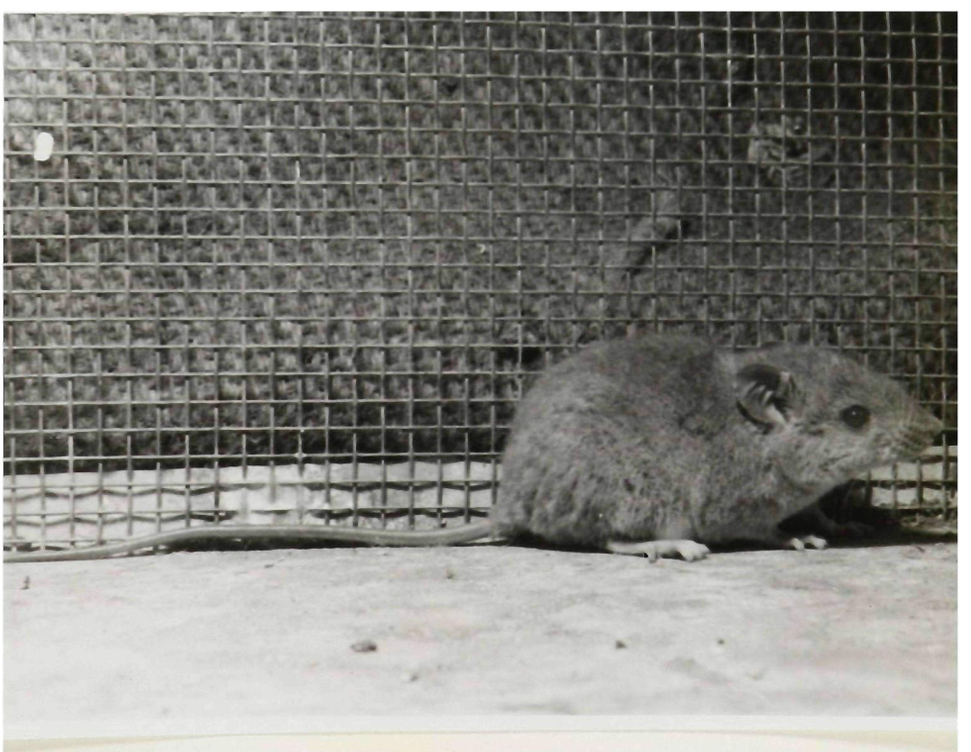


Plate 2. Adult female Melomys cervinipes

Plate 3. Adult female Antechinus stuartii

III HABITAT AND GENERAL METHODS

A. Habitat

The study area at Mt. Glorious, 25 miles (40 kilometers) N.W. of Brisbane, was an isolated patch of Sub-tropical rain forest (Plate 4 and 5) about 150 acres (60.5 ha) in extent, at an elevation of about 2000 ft. (610 m) above sea level. The forest had a general southerly aspect, and, though there were numerous relatively flat benches, in general the slope of the ground was steep. To the south and west the rain forest was bounded by sclerophyll forest of Tristania conferta,* Eucalyptus acmenoides, E. grandis, E. gummifera, E. intermedia, and E. propinqua. Its northern and eastern limits were determined by a tar sealed road running along the crest of the main ridge. On the opposite side of the road was pasture land which had become heavily infested with Lantana camara. A remnant strip of rain forest with a dense surround of lantana thicket occupied a gully running through the cleared land (Plate 4).

Eastern Australian rain forests have been classified by Webb (1959) on a physiognomic basis. He described the Mt. Glorious rain forest as (Complex) Notophyll Vine Forest (Webb, 1959, Plate 15, Photo 6). A basic description of this forest type was given in a field key (Webb, 1959, p.561) - "Notophylls and microphylls most common: robust lianas, vascular epiphytes, plank huttresses (Plates 6 and 7) and compound entire leaves prominent; trunk spaces generally obscured by the Aroid Pothos; stem diameters irregular, many av. 2 - 4 ft. (60 - 120 cm) dbh.

* All botanical species named in this thesis were identified by G. Tracey, C.S.I.R.O. Division of Plant Industry, Brisbane.

Canopy level uneven, av. 70 - 150 ft. (21 - 45 m) with mixed evergreens and rare deciduous emergents."

In this type of forest there are no dominant tree species, but often as many as 30 canopy species occur per acre. On the trapping grid the following were the more common species in the two layered canopy; however this list was not exhaustive: Alangium villosum, Argyrodendron actinophyllum, A. trifoliolatum, Cinnamonium oliveri, Citronella mooreii, Cryptocaria erythroxelon, Daphnandra micrantha, Eugenia corrinantha, E. crebrinerva, Ficus watkinsiana (emergent), Gmelina leichhardtii, Laportea gigas, Penantia cunninghamii, Podocarpus elatus, Pseudoweinmannia lachnocarpa, Sloanea woolsii, Tristania conferta. Common in the understory were juveniles of the canopy species, and Actephola mooreana and Wilkiea austroqueenslandica, both the latter being indicative of an intact forest. On the western half of the grid Archontophoenix cunninghamiana (Picabeen palm) was also abundant in the lower canopy and understory (Plate 8), suggesting poor drainage, though such was not obvious at the ground surface. A shrub layer was present only on the eastern half of the grid (Plate 10) where Rhipogonum album and Eupomatia laurina were the two common species, together with the seedlings of the canopy species. Calamus mulleri (Lawyer cane) was plentiful on the grid, and often formed small, almost impenetrable patches. The common robust woody lianas of the forest were Cissus sp., Legnephora sp., Pandoria sp., Passonsia sp., and Piper sp., and the most conspicuous epiphytes were Asplenium nidus, Platycerium spp., and Dendrobium spp. A close ground cover of herbs was absent, though there were occasional ferns, Doobia aspera, Lastreopsis microsora, and L. minita. In several small areas juvenile palms and cunjevoi Alocagia macrorhiza formed a relatively dense cover 2 - 3 ft. (c.1m) above the ground. (Plate 9).

The forest floor of the study area was of two distinct types. The western half had a good depth of soil (Plate 7), while the eastern half was a jumble of angular basaltic boulders with no soil apparent (Plate 10). There was a scattering of leaf litter throughout the year, but the bulk of the debris lying on the ground was broken twigs and branches, and dead palm fronds with their large flanged bases (Plate 7). Rotting logs and palm trunks from windfalls were relatively common.

B. Trapping

This section describes the general methods employed during trapping periods; specific details are given, where necessary, in appropriate sections.

The traps (Plate 11) used were all of the can-trap type modified from the design described by Davis (1956). Modifications consisted of using 12 gauge spring steel wire for the trigger wire, adding several concentric circles of wire to increase the area of the trigger baffle, using a solid door except for a small hole through which the mouse trap wire passed, adding a spring catch to hold the door shut, and increasing the length of the first section of the trap to 1 ft. (30cm) so that the rat's tail was inside the trap before the animal could work the trip mechanism. The bait was placed just far enough (about 2 ins. (5cm)) behind the baffle so that to reach it the trip mechanism was operated.

A double bait of sweet potato soaked in linseed oil and bacon pieces was used. Linseed oil was found to be the best bait for rats by McDougall (1944a), and in preliminary trials at Mt. Glorious proved to be the best bait for the two rodent species; however bacon was found to be the best bait for Antechinus. Sweet potato was used to soak up the linseed oil rather than pieces of leather, used by McDougall,

since it could be, and readily was, eaten by the rats.

The traps always contained sufficient sawdust to soak up any urine passed, and during colder weather narrow trimmings of soft crepe paper were put in the traps on trap nights. Even with these precautions several Antechinus died in traps, apparently from cold probably coupled with lack of sustenance, since Antechinus rarely ate the bait provided, though apparently they were greatly attracted by its smell.

A rectangular grid 350 ft. x 250 ft. (107 m x 76 m) was laid out in the forest. The perimeter of the grid enclosed an area of two acres. Trap stations were marked with numbered pegs at 50ft. (15m) intervals. Traps were set out singly at each station within a 3 ft. (1m) radius of each peg, depending on the contour and surface of the ground (Plate 11). Trapping on this grid ("grid trapping") was carried out from September 1963 to April 1966. Traps were set for three consecutive nights every two weeks from September 1963 to March 1964; two consecutive nights every two weeks from April 1964 to November 1964; and one night every week from December 1964 to April 1966. When not in use traps were left latched open, in position, and prebaited.

Trap stations were also pegged out at 100 ft. (30m) intervals in a ring 100 ft. (30m) out from the grid edge. (Fig. 1). Trapping at these stations ("ring trapping") was carried out from early April to late November 1964. Traps were set twice a month on the night following the regular fortnightly "grid trapping". These traps also were left latched open in position and prebaited when not in use.

From early March 1965 to mid February 1966 three 1400 ft. (427 m) and one 1000 ft. (305 m) trap lines, with trap stations at 200 ft. (61 m) intervals (Fig 1), were operated ("line trapping"). Once a month ten traps

were set at each station within a 5 ft. (1.5 m) radius of the station peg. The outer station on each line was set first, and each night the traps were moved to the next station nearer the grid. These traps were lifted from the area after each monthly trapping sequence.

Following a few preliminary nights trapping with traps set on trees, a regular trapping sequence on trees ("tree trapping") was carried out from March 1966 to February 1967. When not in use these traps were left in position latched open. The traps were set in position on a board. To the underside of the board was screwed an iron spike which was driven into the trunk of the tree.

In March, June, September and December 1966 additional trapping was carried out on the grid to determine periodicity in activity of the animals. In this trapping sequence ("activity trapping") traps were set for 24 hours every other day for three days. Traps were visited every 3 hours during each 24 hour trapping period, and animals captured were released and traps reset. These traps also were left latched open in position when not in use.

Except in the above "activity trapping" sequence, traps were set at dusk and cleared in the morning, as soon as it was light enough to progress through the forest.

The times of setting and clearing confined animals in traps for the minimum period that was practical, and were essential in avoiding heavy trap losses of Antechinus stuartii, since this species was rather susceptible to long confinement in traps, particularly on colder nights. Separation of lactating females from their litters also was minimised by this procedure.

C. Marking

Several methods of marking individuals were tried. At the

commencement of the study the two rodent species were earmarked by means of a leather punch and using a system of coded ear notches. However the code required punch holes, as well as peripheral notches, and these often became torn. Toe clipping was used to replace punch holes in the code until monel metal fingerling tags were obtained. Fingerling tags were then used exclusively on the rodents, and only two known instances of tag loss were recorded.

A. stuartii was ear marked, using a poultry punch, with the same system of ear notches as for the rats, and,as with the rats,toe clipping had to be used instead of punch holes. Fingerling tags were too large for A. stuartii,and tended to tear out of the delicate ear pinna. Monel metal rings (Linn and Shillito 1960) were not satisfactory owing to the rapid growth rates, particularly in males. This necessitated changing rings when they became tight. After a short trial period these rings were no longer used.

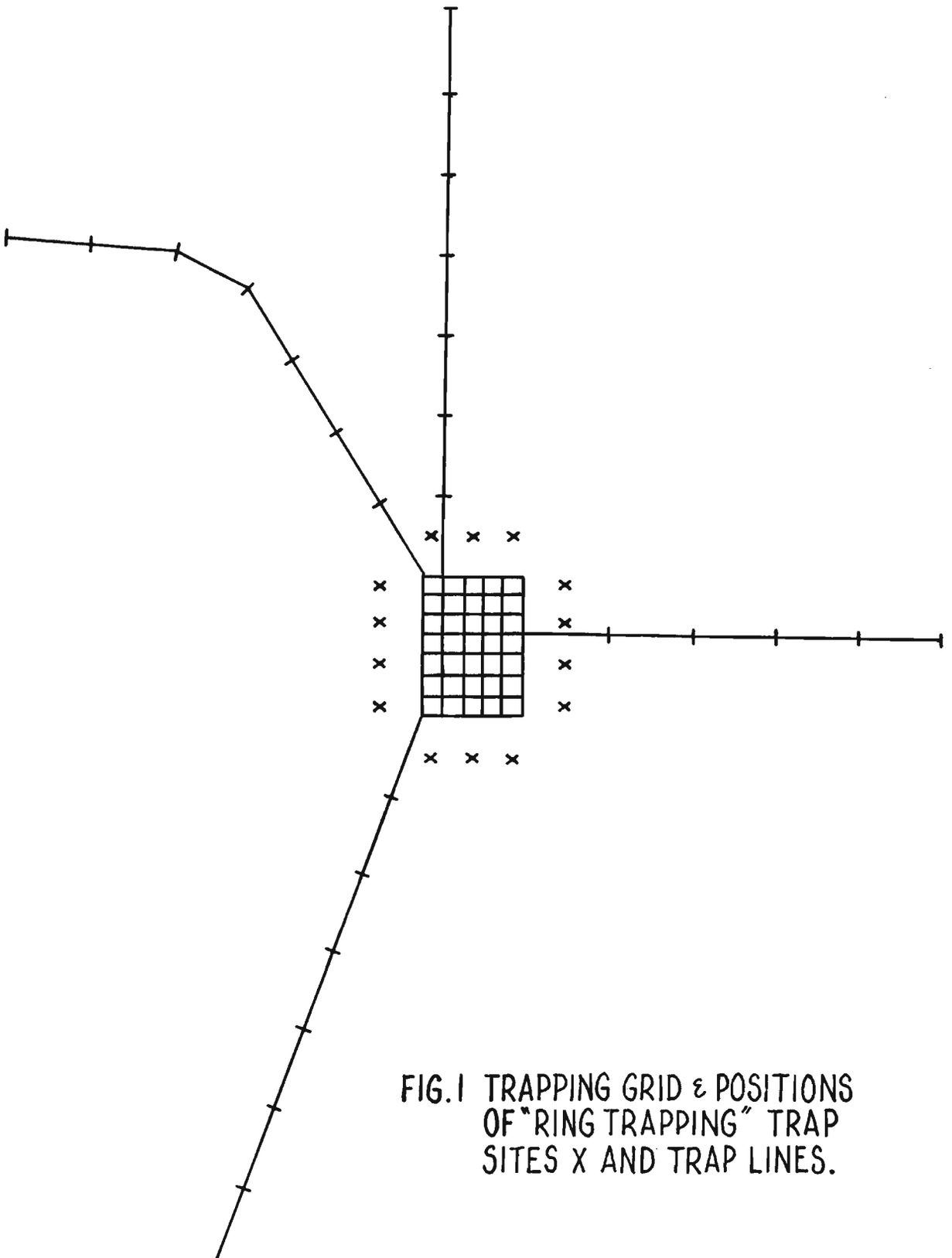


FIG. 1 TRAPPING GRID & POSITIONS OF "RING TRAPPING" TRAP SITES X AND TRAP LINES.

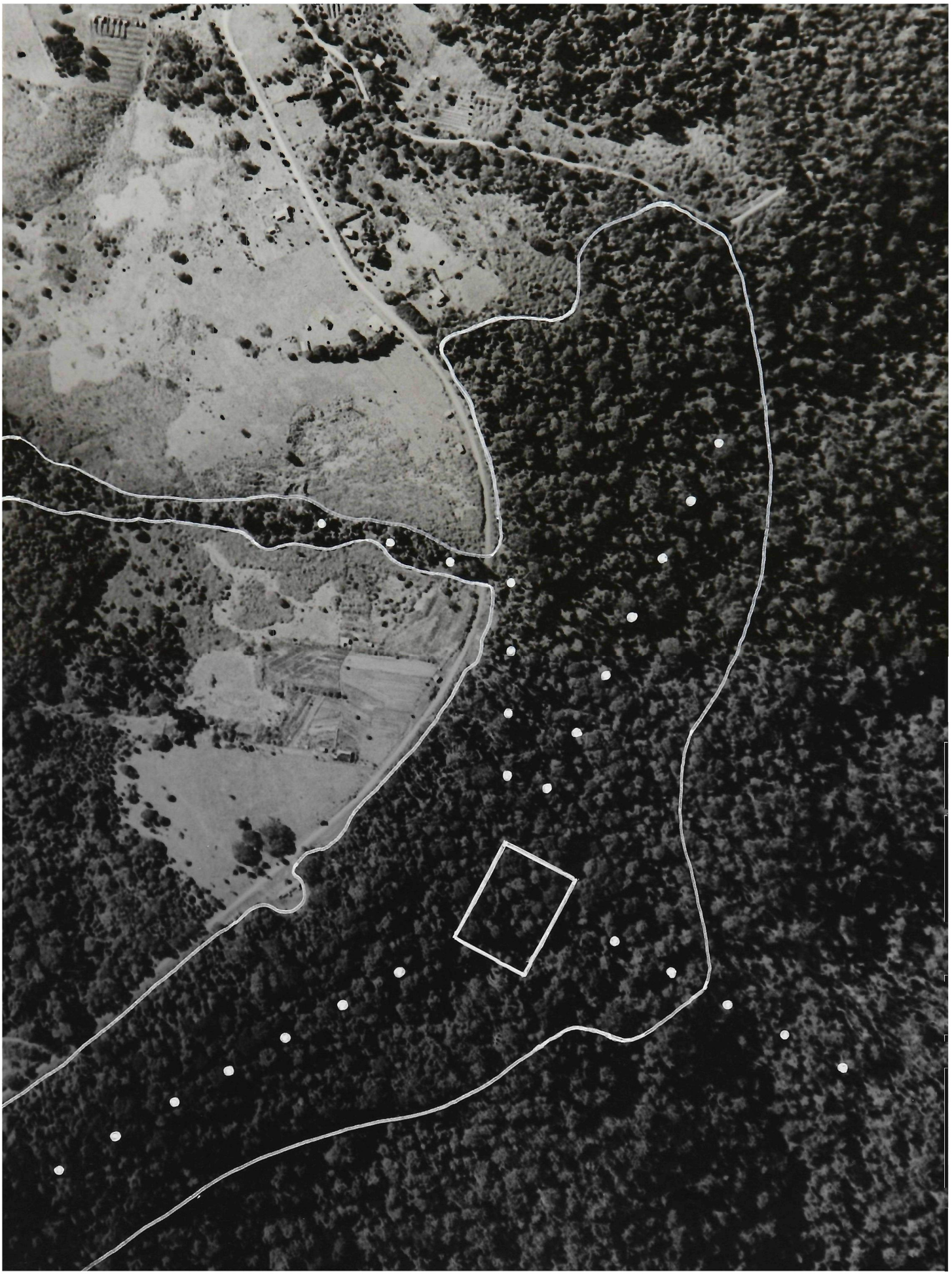


Plate 4. Aerial photograph of study area and surrounds, Mt. Glorious. Rainforest, trapping grid and trap lines outlined.

Plate 5. General view of the rain forest in the study area showing young palms in the foreground and the aroid Pothos sp. on small trees in the centre mid-distance.

Plate 6. Woody lianas hanging from a large tree on the extreme left.

Plate 7. Western half of grid showing buttress roots of a young Sloanea woolsii and soil of the forest floor littered with leaves and twigs and a palm frond with large flanged base. Note absence of a dense shrub layer.

Plate 8. A group of palms (Archontophoenix cunninghamiana) on the western half of the grid.

Plate 9. Cunjevoi (Alocagia macrorhiza) and young palms right foreground form patches of low cover. Large tree on right is Ficus watkinsiana. Also shown is shrub layer typical of eastern half of the grid.

Plate 10. Eastern half of grid showing rocky nature of forest floor and top centre a "tree trapping" board, without trap, on one of the small trees.

Plate 11. Trap in position at grid trap station 5F.

IV BREEDING SEASONS

All breeding information is based on data collected from live animals trapped in the field and released back into the population after examination. Owing to the size of the area under study (the 2 acre (0.8 ha) grid plus the area sampled by the trap lines), the numbers of animals examined at each trapping was often small (Appendix 1 and 2). Thus the graphs in figure 2 on the prevalence of pregnancy may only give a rough indication of the breeding season and intensity for the populations throughout the Mt. Glorious area. But, since most of the resident trappable animals on the grid, except for M. cervinipes, were caught regularly, thus allowing the compilation of an unbroken series of reproductive records for each individual, it was thought the results were a relatively good indication of the breeding which took place in the "grid populations".

A. Methods

Female rats were palped for pregnancy, and the nipples examined for sign of lactation. Only in a few instances was it possible to express milk from lactating R. fuscipes. This was in marked contrast to M. cervinipes and A. stuartii, where milk could be expressed easily from lactating individuals.

The criterion for determining lactation in R. fuscipes was the appearance of the nipples and surrounding body hairs. On non parous females the nipples were very small, and not seen easily even on parting the ventral pelage. During the first pregnancy of caged individuals they elongated to about 3 mm, were relatively thin, and normally covered by the surrounding hair. Following one or two days of suckling by the young,

the hair became pushed back from around the nipples,which were now much fatter,though still only about 3 mm long. The nipples could be seen plainly without disturbing the body hair,and there was a noticeable bare circle of skin around the base of each nipple (Plate 12). Nipples remained in this state throughout lactation. About one week after weaning the skin of the nipples became scaly in appearance, the nipples shorter, and the bare skin around the base of each nipple no longer stood out. The body hairs again covered the nipples,and to see them the pelage had to be parted by hand (Plate 13). During prolonged periods of non breeding, nipples of parous females became very small,but relatively easy to see on parting the ventral pelage,and such animals could be differentiated from non parous sub-adults,even when they were of similar body size.

Male animals were examined for scrotal or abdominal testes,but no standard measurements of testis size were taken.

B. Rattus fuscipes

(i) Results

During the $3\frac{1}{4}$ years study 197 female and 268 male individuals were handled. Pregnant or lactating females were encountered in every month except August,and in a small snap trapping survey programme one lactating female was captured in this month. Notwithstanding this, R. fuscipes had a definite main breeding season,as judged on the percentage of adult females which were pregnant or lactating in any particular month (Fig. 2).

The breeding season commenced in November in 1963, 1964,and 1965 with the exception of one animal in 1964,which became pregnant in September,and lactated through October. During December and January most adult females were breeding,but from February onward the percentage of

adult breeding females showed considerable variation between the three years. In the 1963/64 season the four females handled in February were all pregnant or lactating, but by the end of April breeding had ceased among the adults. The 1964/65 season was notable in that breeding continued well into the winter months, with one individual still lactating in July, though most had finished breeding by the end of May. In 1965/66 the breeding season was remarkably short, and most animals had stopped breeding by the end of January. The average number of young per litter, in 13 litters born to pregnant females brought into the laboratory, was 4.4 (Table 19, section IX). Both in 1963/64 and 1964/65 a few sub-adult females bred towards the end of each season. Most of these individuals had been caught as juveniles early in the season.

No seasonal reproductive changes occurred in adult males, judged on whether testes were in the abdominal or scrotal position, but the numbers of adult males in the total male population varied seasonally. Once the testes of an individual had fully descended into the scrotum, they were rarely retracted back into the abdomen. The few individuals in which the testes did become abdominal were almost invariably caught at the end of the breeding season (Appendix I). Both in the 1963/64 and 1964/65 breeding seasons the testes of a few of the subadult animals became scrotal. In all cases except two this happened in the winter months of May to August. Thus, as in the case of females, a few individuals born early in the breeding season reached sexual maturity at the end of the same season. By September all the males from the previous breeding season could be classified as adults, with fully descended testes, except for the young of winter litters, such as in 1965, when several late young were still subadults with abdominal testes in September and October.

(ii) Discussion

The reproductive biology of R. fuscipes has been studied by Taylor (1961), in Eucalyptus forest in coastal New South Wales just north of Sydney, and by Warneke (1964) in Pinus radiata plantations in Gippsland north east of Melbourne, Victoria. Taylor concluded (p. 19); "Breeding is then essentially nonseasonal, although there may be fluctuations in the amount of breeding activity in the course of a year. As many young are born in March, April, and May as are recorded in all other months put together ..., but whether this peak is real or circumstantial cannot be determined without more data". Warneke's data, however, showed a definite breeding season for this species in Victoria, limited to the months November through February, with the peak in December and January; and this corresponded well with present findings, except that at Mt. Glorious the season extended further into the autumn and winter. Since Warneke used only data from pregnant females, while Mt. Glorious figures included lactating animals, for true comparison with Mt. Glorious the breeding season recorded for Victoria should be extended by another month, i.e. the length of normal lactation. Breeding seasons in the two areas were then almost identical.

McDougall (1946 a) found seasonal breeding occurred in Rattus conatus in the cane fields of the Mackay district, north Queensland, for the years 1937 - 40, though in caged animals over the same period breeding occurred throughout the year, with peaks in summer-autumn and spring-early summer. He considered that breeding was related to rainfall (p. 39); "In normal years there is a rough relationship between rainfall and actual peaks of breeding within a breeding season." In Malaya Rattus species bred more or less continuously in the field, with broad fluctuations, but no clear cut breeding season (Harrison, 1951), and the fluctuations

seemed to be related to rainfall (Harrison 1952). However, at Mt. Glorious correlation of breeding with rainfall (Fig. 2.) could only be considered to occur in the very broad sense that in the summer, when the greatest proportion of animals were breeding, the rainfall was usually higher than in the winter, when breeding virtually ceased.

The mass of data collected on rat populations throughout the world was reviewed, and collated, by Davis (1953). Most of the data referred to Rattus norvegicus, which, on the whole, had no definite breeding season, though there were peaks of breeding activity usually in spring and autumn. Breeding data on R. rattus showed bimodal peaks, continuous uniform breeding, and unimodal curves with late spring early summer peaks. The data presented by Davis were not analysed in detail for relation to climate because adequate microclimate data were lacking. However it is interesting, when considering the breeding information from Mt. Glorious, to note Davis's comments on the data from India, Egypt, and Hawaii (p. 384); "The curves for five places (in India) are generally unimodal, with minima in the cold dry season, although data from Belgaum and Punjab showed additional peaks in the monsoon season. Data from Egypt (Petrie and Todd, 1923) show a definite season of low reproduction in winter. Even on the Hawaiian islands, which have a relatively uniform climate, Eskey (1934) found a pregnancy rate of 0.25 in August, in contrast to a prevelence from November to January (winter months) of about 0.04." Thus in the genus Rattus breeding is essentially non seasonal, but in India, Egypt, and Hawaii for R. rattus, and in Australia for R. fuscipes, a more or less definite seasonal breeding pattern occurs as a result of climatic influence, either directly, or possibly through food supply.

No seasonal pattern of fertility in adult males was observed at Mt.

Glorious. McDougall (1946 a) found that males of R. conatus were also fertile throughout their adult life, and during the colder months of June and July the testes of many field and caged animals ascended into the abdomen without undue loss of fertility. Four of the five species of Rattus studied by Harrison (1955) in Malaya showed a seasonal fluctuation of fertility in the total male population, though even in the winter, when fertility was lowest, the testes of at least 50% of the animals examined contained sperm. However, Warneke (1964) found that the proportion of fertile male R. fuscipes varied from 0 in winter to 100 percent in late spring - early summer in Victoria. The seasonal cycle was the result of three main factors:-

(1) the annual crop of young males, though of adult size, did not attain breeding condition until the spring following their year of birth,

(2) few males survive longer than 12 months i.e. into their second winter, and

(3) those males which did survive into their second winter underwent a sexual regression at the onset of winter due to old age, and this condition was exhibited quite typically by a shrunken, flabby, and discoloured scrotum. Those animals which survived their second winter at Mt. Glorious did not show this scrotal condition during their second winter, though whether or not the testes of these animals contained sperm was not investigated.

C. Melomys cervinipes

(i) Results and Discussion

Extensive data on this species were not obtained because of difficulty in trapping this species.

As with R. fuscipes, August was the only month during the live trapping where no female was caught in breeding condition, but one pregnant

individual was snap trapped in that month. It appeared that M. cervinipes had a more or less definite breeding season which started in September, two months earlier than R. fuscipes, and which might last through to the winter months (Fig. 2). A few young animals bred in the same season as their birth. Two of these were among the few animals of this species to be repeatedly recaptured, and both had two litters in the year of their birth before going into a nonbreeding condition during the winter. This was in contrast to the R. fuscipes subadult breeders, which were observed to have only one litter before their winter nonbreeding condition set in.

The average number of young per litter, in six litters born to pregnant females brought into the laboratory, was 1.8 (Table 19, section IX).

Adult males with fully descended testes were trapped in all months. As in R. fuscipes a few adults were captured which had abdominal testes. These animals did not occur in any particular season.

D. Antechinus stuartii

(i) Results

A. stuartii females necessarily bore only one litter a year, and the synchronous occurrence of births throughout the population was remarkably constant for the three breeding seasons studied (Fig. 2). During these three years 202 females were handled, none of which were in breeding condition outside the months September to February. 82 individuals were caught in these five months, 15 in 1963/64, 29 in 1964/65, and 38 in 1965/66. Most of the young were born in the last week of October, and the litter size during these three seasons averaged 7.5 young per female. No births were recorded before October 21st, and no animals without young in their pouch were captured after October 27th except for three animals; one on October 28th which had a poorly developed pouch and nipples, and had obviously failed to reproduce successfully, and two others caught the

same day which had well developed pouches but no young, though at subsequent captures both had pouch young (Appendix 3).

The young were carried in the pouch for almost exactly 5 weeks before being placed in a nest for further suckling. All animals captured during November had young in the pouch except two captured November 30th which were lactating, having already deposited their young in a nest, and one which had suffered trap injury resulting in the loss of her young. No animals caught from December onwards had young remaining in the pouch, and from then until early February milk could be expressed from the teats of all captured animals, except a few in which the pouch had regressed almost to the non-breeding condition, probably due to loss of the litter. Lactation ceased during February, but the times at which various individuals stopped producing milk varied. Though the pouch and teats appeared in full milking condition at this time, only an almost clear fluid could be expressed from the nipples. It was not known whether this was suckled by the young or not; but, in figure 2 and appendix 3, animals secreting this fluid have been recorded as lactating. One female, whose young were marked while still in the pouch, continued to produce milk up to February 25th, though three of her young were caught in traps during the last week of January, and all her young had been caught at least once by February 18th. It appeared that suckling continued well into the period when the young had begun to forage for themselves. Adult females caught in March all had much reduced teats and pouch area, and no clear fluid could be expressed from the teats. Most of these animals disappeared, presumed dead, during the autumn and winter, but a few survived to breed a second time.

Females breeding for the second time were identifiable from non parous animals on examination of the pouch area. The nipples of those which

had reared a litter, though small, could always be easily seen on parting the covering hairs, while in non parous animals the nipples were not readily visible until the pouch commenced to develop during pregnancy. In the 1963/64 breeding season there was one 2 year old animal among the 15 breeding females captured on the grid. The following season there were two 2 year olds in the total of 29 breeding females caught on or just outside the grid area, but in 1965/66 six of the 10 breeders resident on the grid were 2 years old, and among the 28 females caught on the trap lines 10 were 2 years old.

A total of 264 males were captured during the study, 111 of them within three months of weaning. The testes of all captured males were always in the scrotal position from the time of their first capture. They bred only in the year of their birth, since none survived past their first breeding season (see Section VIII). Changes observed in males in August and September (just prior to breeding) were an increase in body weight (see Table 4, p.48), an increase in the staining of the fur around the sternal gland, and, in a few individuals, a patchy loss of coat from shoulders and rump in late September.

(ii) Discussion

Marlow (1961) studied reproduction in A. flavipes (=A. stuartii, Wakefield and Warneke, 1967). Animals were captured in the field near Sydney, New South Wales, and mating occurred only during a restricted period at the beginning of August, though opportunities to copulate throughout the year were frequent. The gestation period timed from first mating to birth averaged 31.5 days (max 33, min 30 days). During the first 40 days of pouch life the young remained firmly attached to the teats, but after this period they could move from teat to teat. At 70 days they relinquished the teats for longer periods and sometimes rode on the back of the mother. Finally at 90 days they became fully independent.

Degeneration of the pouch was protracted, the hypertrophied condition persisting for about 35 days after suckling had ceased, and a further 30 days was taken for the pouch to return to its normal inconspicuous condition.

Woolley (1966) also studied the reproductive biology of A. stuartii in the laboratory, her animals being captured in the field near Canberra. She confirmed that breeding takes place only once a year, but found that mating took place over a more extended period (July to September) than Marlow recorded. Also the gestation period was found to be more variable. When timed from the day of last copulation it ranged from 26 to 35 days and an even greater variation occurred when timed from the first copulation. Ovulation was shown to be spontaneous, and she suggested that A. stuartii was probably monoestrous. Young remained attached to the nipples for 35 days, then intermittant suckling continued for approximately 90 days. In the laboratory some animals lived long enough to breed for a second time.

Field observations at Mt. Glorious agreed with both these studies with regard to length of pouch life of the young (5-6 weeks). Further, Marlow's observations on pouch regression after lactation suggested that most of the young at Mt. Glorious were probably not suckling during February, when only a clear fluid could be expressed from the teats of the adult females. At Mt. Glorious this would give a period of about 90 days for lactation, similar to the laboratory studies. However duration of lactation was variable, and milk was present in the teats of one female up to February 25th.

The striking shortness of the period within which births occurred at Mt. Glorious supported the suggestion by Woolley that the species was

monoestrous, since, if it were polyoestrous, a more extended season for births would be expected. The short season for births was also in agreement with Marlow's observations on the brief duration of the mating period, but was at variance with Woolley's statement (1966, p.287), "Births in A. stuartii are known to occur in August, September and October .....". However, artificially lighted laboratory conditions may have brought about this variation, since field observations in Victoria (Wakefield and Warneke, 1967) showed (p.95); "Birth occurs at about mid-September. The actual date was recorded in one instance ..... September 14th - 15th," and (p.95), "..... subsequent to October 20th (i.e. 5 weeks later) the pouch area of all lactating females trapped was found unoccupied". Further field evidence from near Sydney in support of early to mid-September as the time of birth was presented by Horner and Taylor (1959). They captured 6 adult female A. stuartii, misnamed A. flavipes in their paper (Wakefield and Warneke 1967), between August 4th and 20th, in which the pouch area was developing but contained no young, and another female on September 5th carrying 4 young, possibly born as early as late August.

Thus there appeared to be a definite difference in the time of breeding in this species between Southern Queensland and the area from about mid New South Wales south. In Southern Queensland breeding occurred 1 1/2 to 2 months later than in the more southerly regions. That breeding occurred later at Mt. Glorious could possibly be correlated with food supply. As so thoroughly discussed by Lack (1954)

adequacy of food for the breeding adults and maturing young appears to be the most important 'ultimate' factor to which breeding seasons are linked.

Antechinus is almost entirely insectivorous. In Southern Queensland the seasonal upsurge in insect populations takes place in summer, owing to the rainfall pattern of usually dry winters and springs, and wet summers. In southern New South Wales and Victoria the rainfall is spread fairly evenly throughout the year with a slight peak in winter (Kendrew 1937), so that the upsurge in insect populations comes with the spring and early summer, i.e. earlier than in Queensland. Thus it would be decidedly advantageous for the southern populations of A. stuartii to breed earlier than those in South Queensland.

E. Combined pattern of breeding in the three species

Reproductively the three species were a rather varied group. The two rodents were polyoestrous, but A. stuartii was monoestrous. R. fuscipes had a moderately sized litter (average 4.4) and comparatively short breeding season (late November - April), but M. cervinipes had a small litter size (average 1.8) and relatively long breeding season (September - April). Both rodents weaned their young at about four weeks old. On the other hand A. stuartii had a large litter size (average 7.5) and very long nursing period (about 4 months). However, as a whole, breeding was restricted to the spring, summer, and early autumn. The different dates within this period at which each species commenced breeding seemed to be adjusted to the nature of their food and its supply, in relation to their varied individual reproductive biology.

In the south Queensland rainforest the abundance of insects and fruits is seasonal - e.g. the common "sub-social" rain forest beetles of the family Passalidae breed in the summer, and their larvae are common in crevices and on the undersides of rotting logs from January to March

(Monteith, pers. comm.); large crickets Anastosoma sp., Stenopelmatidae, and also Tettigoniid species are noticeably abundant from January to April; and palm nuts and figs litter the forest floor in March and April (personal observations).

R. fuscipes was the last to commence breeding, but despite the late start the first young appeared in the traps a little earlier than those of A. stuartii, an early breeder. Normally young continued to enter the population up to about the end of April. The diet of R. fuscipes consisted of vegetable matter, some fruit and, particularly in the summer, about 50% insects (Harrison 1961, Warneke 1964). Thus the timing of the start of breeding, two months later than the other two species, was adjusted so that most of the young were weaned at the time of the seasonal abundance of their main food supply.

The breeding pattern of M. cervinipes could be related to its diet of mainly shoots and leaves (Harrison 1961) and small litter size. The supply of this type of food was relatively constant in the forest. Thus an early spring start (September) to breeding followed by a protracted breeding season was advantageous, since, together with a small litter size, it resulted in a steady entry of weaned young into the population, adjusted to the steady food supply.

The insectivorous A. stuartii also started breeding early in the spring. This early start could be attributed to the length of the gestation period plus nursing period (4 - 5 months). Thus the young were not weaned until late summer (February) which was later than the time of weaning of the first young of the two rodent species. Nevertheless it was a time at which insects were abundant.

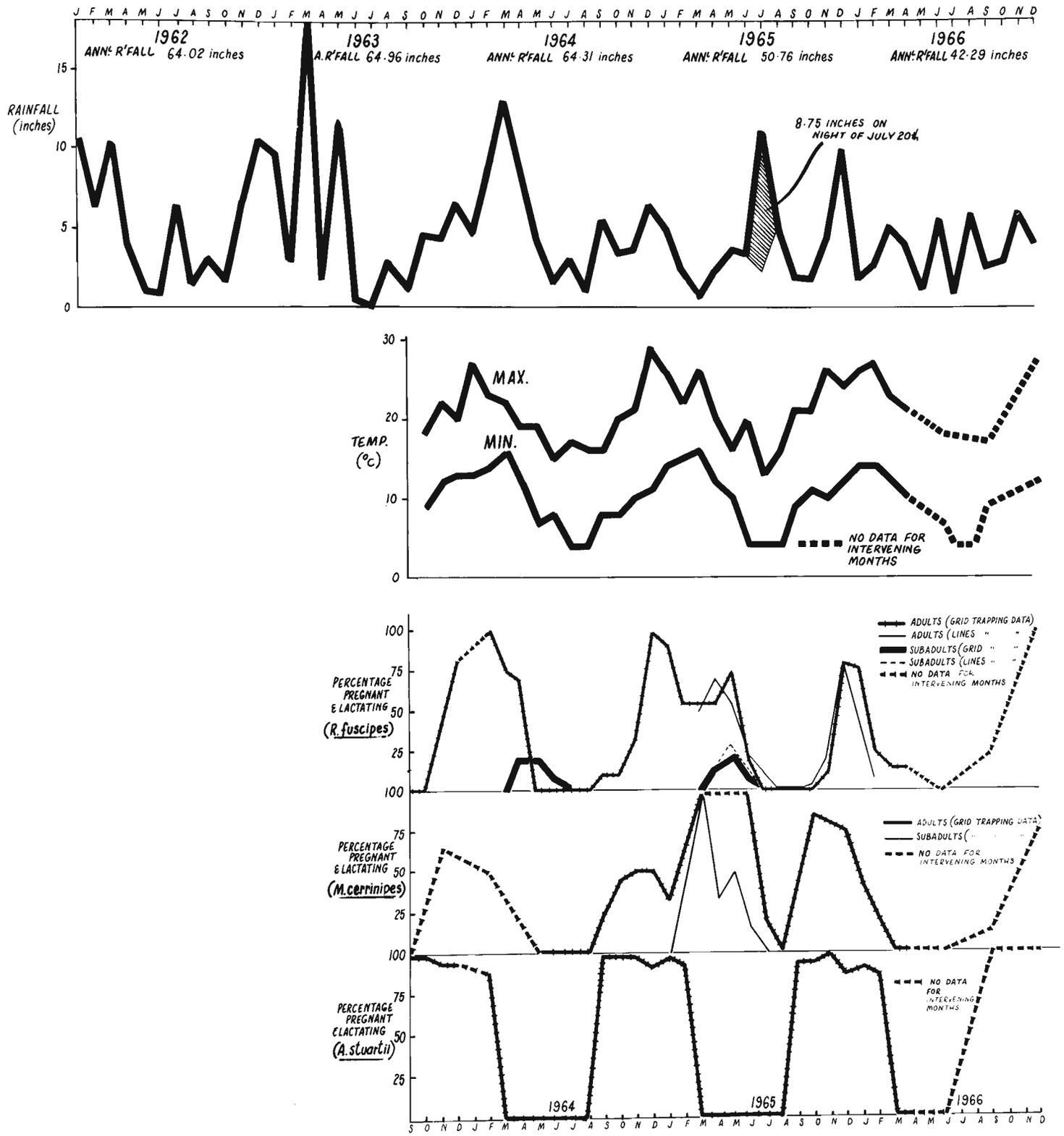


FIG. 2 BREEDING SEASONS OF R.FUSCIPES, M.CERVINIPES, & A.STUARTII; MONTHLY RAINFALL, & MAXIMUM & MINIMUM AIR TEMPERATURES AT GROUND LEVEL.

Plate 12. Lactating R. fuscipes showing how ventral pelage becomes pushed back exposing the short fat nipples and bare patch of skin at base of nipples.

Plate 13. Post lactating R. fuscipes. The position of the nipples can still be seen but the ventral pelage covers them from view.

V. LABORATORY EXPERIMENT ON MORTALITY OF MALE A. STUARTII FOLLOWING BREEDING

The most striking feature of the biology of this species was the death in the field of all adult males at the end of the short breeding season. Woolley (pers. comm. and 1966) in her study of A. stuartii found that males, trapped earlier in the year, and maintained in the laboratory up to five months after the end of the mating season, underwent a rapid decline in condition, and many animals died. She also observed that before the onset of the breeding season body weight of males increased rapidly. During the breeding season body weight fell, and by the end of the season was down to, or below, what it was before the rapid rise. No records were kept on whether males which survived the breeding season had been caged with females or not.

In the light of these results, together with the field evidence from Mt. Glorious that every adult male in the field died about two weeks before the young were born (see section VIII), it was thought that death was possibly due to one, or a combination, of three factors:

1. General changes in the males physiological processes associated with breeding;
2. Physiological stresses resulting specifically from mating;
3. Behavioural changes in males and/or females during or immediately subsequent to the breeding season.

A laboratory experiment was set up to investigate the last two possibilities.

A. Methods

The experimental animals were kept in cages 10" x 12" x 18" (25cm x 30cm x 45cm) made of galvanised sheeting except for the tops and backs which were of $\frac{1}{4}$" (6.4mm) wire mesh. Each animal was provided with a nest box 5" x 5" x 5" (12.5cm x 12.5cm x 12.5cm) also made of galvanised iron, and lined with $\frac{1}{2}$" (12.5mm) thick "canite" board. Each nest box was attached to the outside of the cage (Plate 14). An activity wheel was placed in each cage, and fresh leaf litter from the rain forest was provided as bedding material every one to two weeks. Food and water were presented ad lib. The basis of the diet was freshly killed white mice; meal worms were fed once a week, and large grass-hoppers and cockroaches every two or three days depending on the supply. The animals were housed under natural light conditions, and the ambient temperature of the animal house kept as low as possible. However, during the last week of September the temperature for six hours of the day (11a.m. to 5p.m.) averaged 30°C, with a maximum at 3p.m. on one day of 33°C. For the remainder of the experimental period the temperature ranged around 20°C, rising to a maximum of 25°C during the hotter days, and falling to a minimum of 15°C on the cooler nights. These temperatures were some 5°C higher than the maximum and minimum monthly readings taken in the rain forest at Mt. Glorious during the same period.

The experiment ran from the first week in September 1965, about 3 weeks before mating normally took place in the field, through to the last week in December 1965, $2\frac{1}{2}$ months after all males in the field had died. That year young were born in the field at the usual time - the last week to ten days of October. Assuming a gestation period of 33 days, the maximum recorded by Marlow (1961), mating must have taken place

some time after September 19th. All the animals for the experiment were caught at Mt. Glorious before September 3rd, and it was therefore assumed that the males had not copulated in the field.

The males were divided up into 4 groups of six. In cages 1 to 6 one male was kept alone in each cage and given no chance to mate with or see female individuals. Cages 7 to 12 contained two males in each and these animals also were never allowed to mate with or see females. Each of cages 13 to 18 contained one male and one female. At the end of September after mating had taken place, the females were removed to six empty cages, where they remained until the end of the experiment. The last set of cages 19 to 24 also contained male/female pairs, but these pairs were left together throughout the experiment.

Animals were weighed at regular intervals of from 7 to 14 days. No attempt was made to duplicate similar sized males or females between the four treatments, since males in the field died irrespective of their body weights.

B. Results

Figure 3 summarises the results of the experiment. All the males except one lived longer than those in the field. Four of the six males kept continuously with a female lived to the end of the experiment; one died mid-October and the other at the end of September in synchrony with those in the field. Four of the males separated from females after mating also lived to the end of the experiment, while one died in the first week of December, and one escaped and was accidentally killed during recapture in the first week of October. In the series of males kept on their own, two lived to the termination of the experiment, one died the week before termination, two died in November, and one died mid-October. In the group with two males per cage, one animal in each

of the cages 7, 8, 10 and 11 lived to the end of the experiment, and the rest all died during mid to late October.

A comparison of the weight changes recorded in the experimental males was made with the weight changes that occurred in males which were recaptured in the field during the course of the general field study (Table 1). To determine whether such a comparison was justifiable or not a Kruskal-Wallis one-way analysis of variance by ranks test (Siegel 1956) was carried out on the weight changes in the males of the four experimental groups. This test showed no difference between the groups in the pattern of weight changes between early and mid September ($H = 2.4$, d.f. 3, $0.50 > P > 0.30$), or between mid- and late September ($H = 4.2$, d.f. 3, $0.30 > P > 0.20$), which could be attributed to anything other than chance variations such as are to be expected among several random samples from the same population. In all instances where the results of t tests have been presented below, F values were not significant at the 5% level.

The pattern of the weight changes in both the laboratory and field male animals was basically the same. There was a relatively rapid rise in weight during early September to a peak in mid September, followed by a fall in weight during the latter half of September, the mating season (Table 1 and Fig. 3). This pattern was normal for males at this time of year (Table 4 , p.48 and Fig. 8). However, some animals in both laboratory and field samples showed no rise in weight, but continuously lost weight during the experimental period (Table 1 and Fig. 3). It appeared that these individuals had matured early, and thus reached their maximum weight one or two weeks before the others, i.e. at the time of the first weighing period of the experiment (August 31st - September 3rd). They were considered to be early maturing animals since, in both the laboratory and field samples, their body weights were significantly higher, when weighed between August 31st and September 3rd, than those of the other individuals of their respective samples (laboratory

Table 1 Body weights of male A. stuartii and cage numbers of laboratory animals.

Field Data				Laboratory Data		
Date of weighings Weight in grammes			Cage no. of males	Date of weighings Weight in grammes		
Aug 31st-Sept 3rd	Sept 13th-Sept 16th	Sept 30th-Oct 3rd		Aug 31st-Sept 3rd	Sept 13th-Sept 16th	Sept 30th-Oct 3rd
40	45	-	1.	48	41	49
41	44	-	2.	46	48	44
54	56	-	3.	38	44	44
43	47	-	4.	38	48	40
50	51	-	5.	35	46	32
54	56	-	6.	41	50	38
57	61	-	7.	46	43	42
38	39	-		45	40	45
40	49	-	8.	-	33	39
38	45	-		-	41	36
34	40	-	9.	41	53	52
36	44	-		36	48	42
47	50	-	10.	40	46	43
45	47	-		58	55	48
38	41	-	11.	53	44	40
45	51	-		60	62	52
50	54	-	12.	51	48	42
58	64	-		46	40	42
57	59	-	13.	48	50	45
28	39	33	14.	42	46	37
28	36	-	15.	52	51	40
34	44	-	16.	38	46	47
36	42	-	17.	56	51	44
45	55	-	18.	38	50	40
33	44	35	19.	41	51	48
63	58	-	20.	36	45	45
57	55	-	21.	32	37	38
57	52	-	22.	34	45	40
65	54	-	23.	35	42	35
65	58	-	24.	36	31	33
57	52	-				
46	44	-				
-	64	45				
-	61	44				
-	50	39				

data $t = 9.58$, 26 d.f., $P < 0.01$; field data $t = 10.40$, 30 d.f., $P < 0.01$). Also, in the case of the individuals in the field sample, where their previous histories were known, all had shown the expected gain in weight earlier in August. The proportion of early maturing animals in the laboratory sample was not significantly different from the proportion in the field sample ($\chi^2 = 0.175$, 1 d.f., $0.70 > P > 0.50$).

Though the pattern of the weight changes in both the laboratory and the field males was essentially the same, there was some difference in the absolute weight changes between the two groups. The loss in weight of the field males during the latter half of September was considerably greater than the loss in weight of the laboratory males ($t = 2.92$, 33 d.f., $P < 0.01$).

Two other facts, one of which has been briefly mentioned previously, were noteworthy in the experimental results. In every case where males were paired with males one of the animals in each cage died during October, and in two cages both of the animals died. The four which remained alive were left unpaired, and all four lived to the end of the experiment.

There was also an interesting difference between the two groups in which males were paired with females. In both groups four of the males lived to the end of the experiment, and the difference between the groups lies in the history of the females. Among the females which were removed from the males after mating and placed in cages of their own, three out of the five (one female having died earlier) produced litters during the last ten days of October, i.e. in synchrony with field births, but none of the females continuously paired with a male were found with young in their pouches.

C. Discussion

If as was suggested, copulation triggered or expedited some change in the

physiological processes Of the males leading to their death, it was expected that the males which had copulated would have died more or less in synchrony with the males in the field, and that those males which had not, might have lived on for an indefinate period. However, four males in each group survived at least two months after the mating period. Thus under the experimental conditions, copulation did not inevitably result in the death of the male. Since most of the males which were paired with females did not die in the laboratory, this indicated that field conditions relevant to male deaths were not being duplicated in the laboratory experiment. These conditions were examined as pointers towards the possible cause of male deaths.

In the laboratory the most obvious differences from the natural environmental conditions were the provision of an abundant and modified food supply obviating the necessity to hunt for food, the removal of predation, the limitation of space, and the isolation of males from each other in three of the four laboratory groupings.

From the comparison of the weight changes in the laboratory males with those in the field males it seemed possible that food might have been involved. The pattern of the weight changes during the breeding season in the field males at Mt. Glorious and in the laboratory males was similar to that described by Woolley (1966), if the reasonable allowance was made that the heavier animals which lost weight throughout September had matured earlier than the others. The pattern of the weight changes therefore could be considered to be normal. However, the fact that laboratory males lost much less weight than field males through the breeding season to the end of September, was suggestive that the abundant supply of food was having a modifying effect on natural body weight changes. Antechinus was almost entirely insectivorous (Harrison 1961, Wakefield and Warneke 1967), and it seemed unlikely that food was in such short supply in

the forest as to be the cause of death; furthermore the females survived in the field. Therefore, if lack of food were the cause of death, it would also have to be postulated that the food was short for the males only. Possibly the mating urge became so great that males in the field ceased hunting for food and became so weakened that they did not recover. No evidence was available for or against this supposition.

The possibility that predation alone could cause the extermination of the males also seemed unlikely. Potential nocturnal predators in the forest were snakes, dingoes, feral cats, and boobook owls. However, since female mortality at that time of year was low (see section VIII), the predation would have had to have been highly selective against the males to cause the 100% mortality. Since the males wandered outside their normal ranges during the breeding season (see section VII), they could have been more prone to predation through unfamiliarity with their surroundings. Also they may have become less cautious under the mating urge. Nevertheless it seemed extremely unlikely that predation alone could have caused the complete extermination of one sex over so short a period.

The effect of the limitation of space in the laboratory on the mortality pattern of the experimental animals was unknown. However, the reduced scope for locomotary activity was countered by the provision of activity wheels, which were used incessantly.

The most likely lead arose from the removal of social contact between males in three of the four experimental groups. Where two males were caged together, one of each pair died, and in two cases both individuals died; but most of the males paired with females, or kept alone, survived. Aggressive behaviour between the males which were caged together was often observed.

Aggressive behaviour between males during the breeding season is common (Beeman 1947, Bronson 1963, Sadlier 1965). Also Woolley (1966) noted, that though young males of A. stuartii maintained in the laboratory showed no tendency

to fight, as they matured they became aggressive, and the aggressive behaviour was intense in reproductively mature males.

Field observations at Mt. Glorious showed that, at least as late as July, males lived together amicably, since three were caught in a single nest of leaves in the roof gutter of a shed, and four males were trapped in the roof of the house of a local resident in two consecutive nights of trapping in July. However, in September males in the field were aggressive towards each other. The only double captures recorded for A. stuartii during the study occurred in September. There were four of these. In each instance both animals were males, and intermittant chattering and scuffling from within the traps indicated aggressive behaviour between the two occupants. In one case fighting between the two animals continued for several minutes on the forest floor after their release. On another occasion in September one male actively attempted, for a period of five minutes, to enter a closed trap within which another male was caught, chattering aggressively as it did so. Though the aggressive behaviour within the traps could be interpreted as resulting from the confinement of two individuals in a small space, the fact that all the double captures concerned males only, suggested that the double captures were the result of chases during aggressive behaviour outside the trap.

Thus aggressive behaviour between males in the field may have reached such a peak during the short breeding season as to have caused some sort of "stress syndrome" that resulted in their death. Whether it was in the form of an adreno-pituitary system breakdown, such as Christian (1950) postulated for population crashes; some sort of "psychological insult" bringing about physiological upsets as suggested by Griffiths, Calaby and McIntosh (1960) to explain contradictory results in adrenal histology of experimental animals which had died from "shock"; or some other form was not determined. Though Christian and Davis (1964) have suggested that "shock disease" has been over-emphasized in relation to population crashes, they also noted that there is a large amount of

evidence to link abnormal changes in the adrenal glands with stress situations.

If "stress disease" is the operative mechanism in this case, we should expect to find that the stresses which eventually overtax the adreno-pituitary system appeared rather suddenly and together during September, when the males died. Of the many forms of stress which Christian (1950) listed as making demands on the adreno-pituitary system, at least four of them - reproduction, increased activity, food shortage, and aggressive behaviour, were all increased or became operative during September. Thus:

1. The mating season was intensively restricted to this period.

2. Male activity increased during this period as evidenced by the increase in the average distance between captures in September (see section VII) and the sudden appearance of many transient males in the population at this time (see section IX).

3. After putting on weight following the winter lull in growth, males, in contrast to females, lost weight during the latter half of September, suggesting, as noted above, that males were undergoing a food stress, possibly due to the mating urge over-riding the hunting drive.

4. Aggressiveness between males occurred during the reproductive period, though before this period males appeared to be passive towards each other (pers. obvs., see above, and Woolley 1966).

Again, if "stress" was the cause of death, as males started dying the intensity of the stress situation between the remaining males would weaken and therefore some would be expected to survive. However, both males and females mate more than once, at least in the laboratory, (Woolley 1966), and the remaining males might overtax their already strained adreno-pituitary system with repeated matings or attempted matings.

Also the lethargic condition into which post reproductive males pass would make them more open to predation, so that predators may help to finish off the stragglers. At Mt. Glorious a few males were captured as late as two weeks

after most of the females must have conceived, and as noted (section VII) these males were in a lethargic condition, and in fact did not survive the journey to the laboratory to which they were being taken.

There was no indication from the experimental results, of female aggressive behaviour towards the male after mating, since as many males survived in the group in which males and females remained paired after the breeding season, as in the group in which male/female pairs were separated after mating occurred.

In the light of the meagre amount of data at the present time on the phenomenon of the 100% male mortality following breeding it is difficult to see how it might have evolved. However, from the few clues which exist a possible course for its evolution will be postulated.

From the evidence that males survived in the laboratory long past the period in which they died in the field, it follows that males do not carry a genetic complement which programmes a physiological life span of just less than one year regardless of other factors either behavioural or environmental. The experimental results suggested that male aggressiveness towards each other, which developed in the breeding season, was the main factor which, by over-loading the adreno-pituitary system, caused the males to die from "shock disease". Therefore it is the evolution of male aggressiveness to the extent that it causes a "stress syndrome" in all males that must be explained.

Four other pertinent facts are known:

1. Woolley (1966) found that though pouch area and body weight undergo similar changes in mated and unmated females, in the latter there was no recurrence of the changes, thus suggesting that females are monoestrous.

2. Woolley (1966) also noted that males which survived in the laboratory to their second mating season showed no changes normally associated with coming into breeding condition and did not breed a second time. Histological examination of their testes showed that degenerative changes had taken place.

3. From the evidence of the increased size of their movement patterns in the field (see section VII) in September, when mating takes place, it is inferred that male animals are promiscuous.

4. Post-reproductive males become lethargic, though they still show hostility towards other males on meeting (pers. obvs. and Woolley 1966).

Now it seems reasonable that since males are promiscuous, a more aggressive male will impregnate more females than a less aggressive male, and therefore, other factors being equal, will make a larger contribution to the gene pool of the following generation. Since females are monoestrous this process will be enhanced. Thus, through differential reproductive success, male aggression will be selected for. Provided that there are no associated deleterious effects, the more aggressive individuals of a generation will always contribute more to the gene pool of the following generation than the less aggressive animals, until the level of aggressiveness during the breeding season reaches an intensity which causes males to die from "shock disease", as suggested above.

One point should be mentioned here. This hypothesis seems to be at variance with the latest theory on the mechanism of population regulation, namely, "..... susceptibility to natural hazards increases among generations descended from animals affected by adverse environmental conditions" (Chitty, 1960 p.105). If Chitty's hypothesis is correct then A. stuartii populations would seem to be in an intolerably precarious position, since any "natural hazards" would be likely to decimate at least the male section of the population before mating took place. In fact the evolution of aggressiveness to the degree suggested would probably not occur.

It may be asked why the adreno-pituitary system does not evolve in parallel with increased aggressiveness so that the increased stress situation can be handled and death prevented. The answer to this question seems to lie in the fact that, after the one short mating season, males are no longer capable of reproduction. Therefore, should any more efficient hormonal system evolve so

that the males which possessed it lived on to the following breeding season they could make no further contribution to the gene pool. Therefore no differential reproductive success would be endowed by the possession of such a character, and consequently no selection for it would occur.

So far it has been assumed that the breeding season was always synchronous throughout the population. One reason for supposing this to be the case is that the breeding seasons of all other members of the Dasyuridae, whose breeding has been investigated, are also comparatively short (Woolley 1966). However, a more spread out breeding season would not affect the argument for the evolution of male aggressiveness. But only with a simultaneous breeding season throughout the population would the intensity of the male aggressive behaviour be likely to be sufficient to cause "stress disease" in all males.

The timing of breeding seasons is selectively fixed so that the young are reared during that period of the year in which the optimum number survive under normal conditions. If aggressiveness in the breeding season is selected for, later maturing males and even females may be killed by early maturing males, since Marlow (1961) has noted that the attentions of reproductively mature males towards unresponsive females are far from gentle. Thus a smaller and smaller proportion of the total gene pool will come from later maturing stock, until all animals mature at the same earliest optimal time. Here again the fact that females are monestrous will greatly facilitate the process.

Thus, selection for aggressiveness can be conceived as a factor which will synchronise breeding, and lead eventually to mass male mortality immediately following breeding.

Since this postulate is dependent on synchronous breeding, it is pertinent to ask what factor or factors could provide the accurate timing

of the onset of breeding necessary for synchronisation. It is well known that breeding seasons in general are remarkably labile in mammals and birds. Marshall (1959), in discussing the control of breeding in birds, clearly set out the most plausible relationships between the internal physiological and the external environmental factors which are involved. Endogenous rhythms are the primary seasonal initiators, and until growth and development of the internal sex organs has reached a certain stage no gametogenesis can take place. When this stage has been reached there is a "spontaneous progression" to liberation of sex hormones and gametogenesis is then possible. From this stage onwards behavioural and physical environmental factors influence the speed of the course to final fertilisation, and it is during this stage that the variability arises.

In the case of A. stuartii, for the four breeding seasons which occurred during the study period, it was apparant that there was no variation in the time of the year at which mating took place. The only environmental factor which is sufficiently regular to give such constantly precise timing seems to be light. Farner (1965, p.360) states: "There is good evidence for a role of photoperiodic elements in the control of ovarian cycles and estrus in at least twelve species (of mammals)", and further notes (p.361): "It is now generally evident in mammals that photoperiodic controls are by no means rigid but rather provide the important precise timing for events that would eventually occur anyway, possibly because of crude endogenous quasi-annual timers".

Thus the breeding behaviour of this small marsupial mouse seems to be of great interest from two points of view - the mode of action of mortality processes in small mammals, and the timing mechanisms of breeding rhythms. This is particularly so since as noted by Jones (1923, p.98), "the Yellow-footed Pouched Mouse is an animal of great interest ----- since in the

whole of its anatomy it shows itself to be a remarkably generalised animal. It represents a marsupial base form, its general anatomy being but little modified from a basal mammalian plan, and it stereotypes the simple creature that could be ancestral to most of the marsupial radiations".

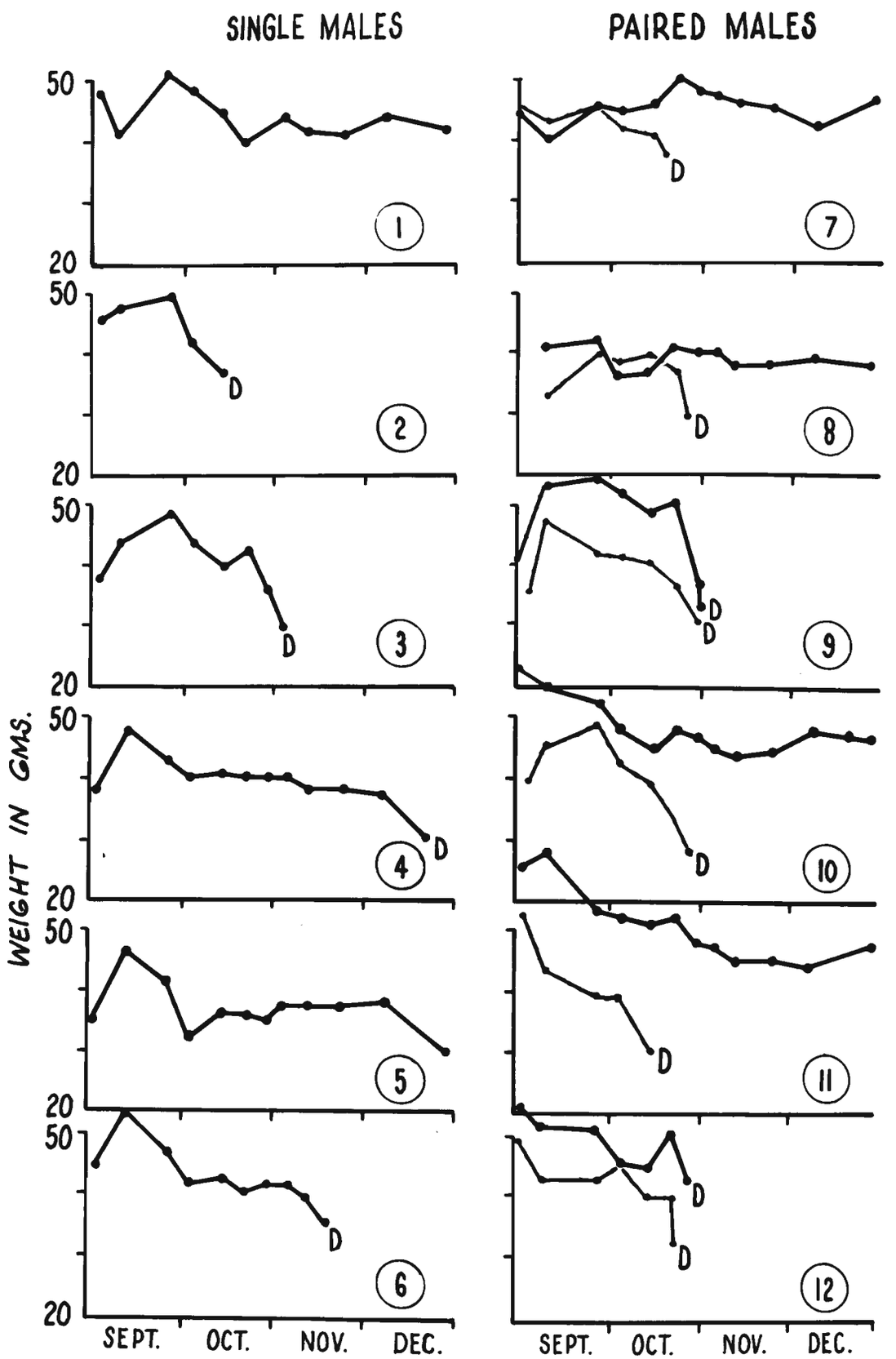


FIG. 3 WEIGHT CHANGES IN THE EXPERIMENTAL INDIVIDUALS OF A. STUARTII.

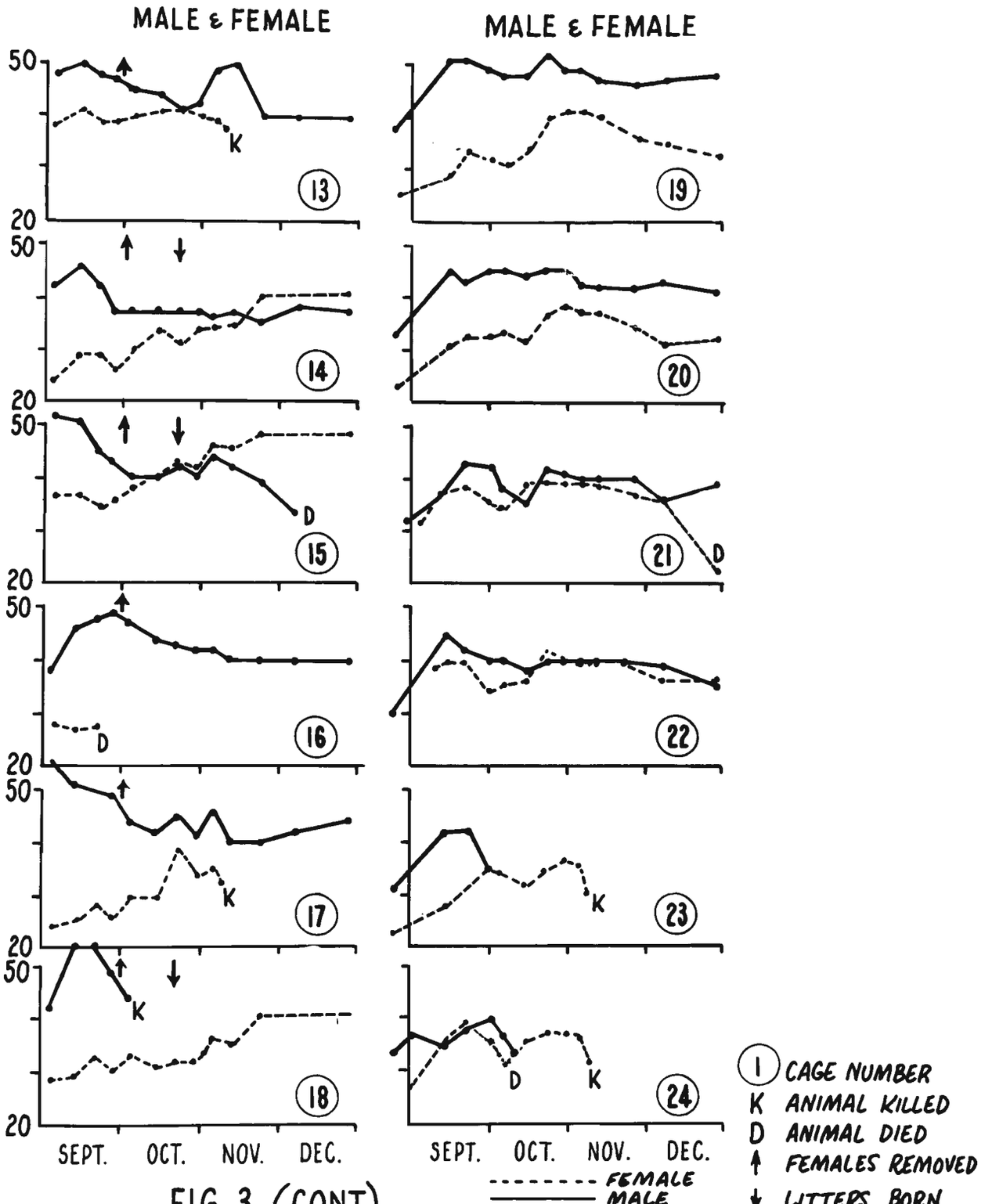

MALE & FEMALE
MALE & FEMALE
50
20
K
13
19
14
20
D
15
21
D
16
22
17
23
18
24
SEPT.
OCT.
NOV.
DEC.
FEMALE
MALE
1 CAGE NUMBER
K ANIMAL KILLED
D ANIMAL DIED
FEMALES REMOVED
LITTERS BORN

FIG. 3 (CONT).

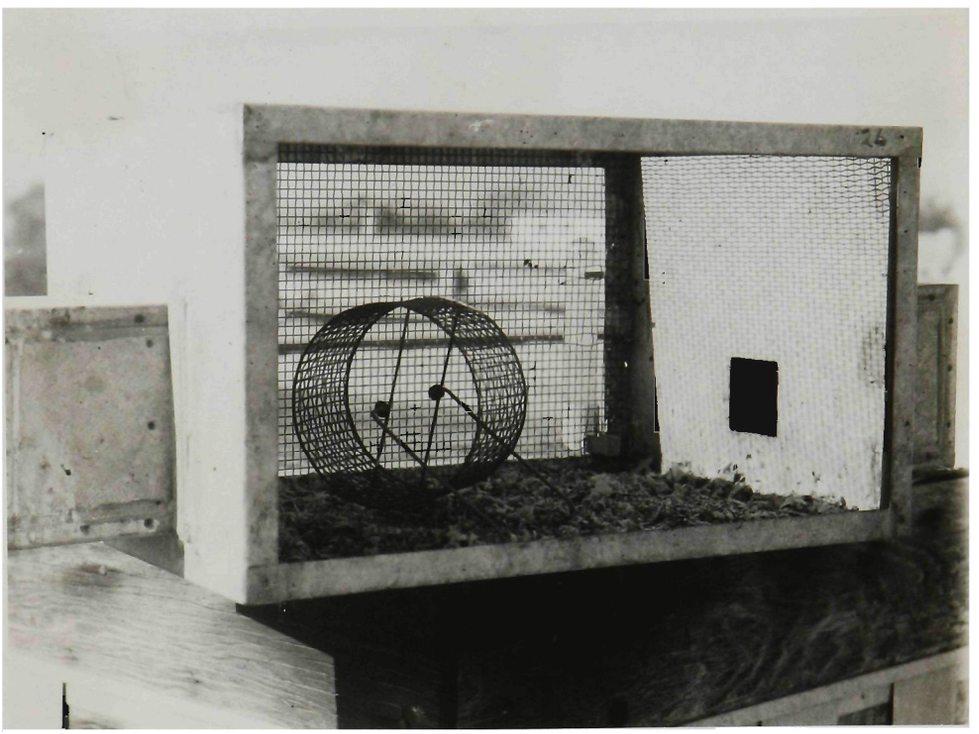


Plate 14. Cage used for housing A. stuartii animals in the laboratory experiment showing a nest box at each end, and an activity wheel. A metal or glass sheet can be slid down from the top to close the front of the cage.

VI GROWTH

A. Rattus fuscipes

(i) Methods

All animals captured in the field during the regular trapping were weighed in a cloth bag with a Salter 200g spring balance which could be read to the nearest gramme. Growth in relation to age was examined by using the data from 31 individuals first caught within one week of having been weaned, and subsequently recaptured several times over a period of from two to six months. Also an analysis was made of the average monthly body weight distribution of the population.

In order to establish which animals in the field had recently been weaned it was necessary to use laboratory data on body weight at weaning. Both Taylor (1961) and Warneke (1964), agreed that weaning occurred at about 28 days. Taylor gave a weight of 30g $\pm$ 10g as the weight of the young at this age, and the growth curve given by Warneke indicates a weight of about 40g at one month old. Two pregnant females caught at Mt. Glorious and brought into the laboratory each gave birth to a litter, one of three young and one of five young. At 28 days old each of the three young of the first litter weighed 25g. In the second litter two of the young weighed 20g and three weighed 19g at 28 days old.

Since the body weights of the young of both these Mt. Glorious litters fell in the range given by Taylor for 28 day old young, her figure of 30g $\pm$ 10g was used to determine which animals in the field

had recently been weaned. The 31 animals (20 males, 11 females) whose body weights were used in composing the average growth curve all weighed between 29g and 40g at their first capture. It was assumed therefore that they were all about four weeks old.

(ii) Results

The growth curve upto six months old showed that, except at the first capture, the average weight of the females was invariably below that of the males (Fig. 4). However, the variation in weight of both males and females at any given age was relatively large (Table 2), and there was considerable overlap between the sexes.

There was a marked slowing up of growth during the third and fourth months after weaning, and by the fifth month there was a definite pause in both sexes. At this time the male weights ranged between 90g and 120g except for one individual which had attained a weight of 132g. Female weights ranged between 90g and 110g. The growth of the laboratory litters, after an initial post-weaning burst, followed more or less at the same rate as the field animals (Fig. 4).

The analysis of the monthly body weight distribution of the whole population showed that few adult females attained a weight of more than 180g, though males of this weight or more were present in the population throughout the year. The pattern of the changes in distribution of the body weights during the year was similar for females and males, and the patterns were repeated in following years (Fig. 5 and 6).

Dealing with females first, it can be seen that when breeding commenced in November most females weighed 111g - 140g. As the season progressed through the peak period of December to January, when most females were pregnant or lactating, body weights had increased, and the numbers of individuals were about equally divided between the 111g - 140g

Table 2. Mean weights in grammes of individuals of known age of Rattus fuscipes.
(N = sample size, M = mean weight to the nearest gramme, S = standard deviation).

	Field Data						Laboratory Data		
	♀			♂			♀ & ♂ combined*		
Age** (weeks)	N	M	S	N	M	S	N	M	S
4	11	38	3.06	20	36	3.25	8	22	2.92
5	2	39	(38-40)+	7	48	2.58			
6	6	46	4.00	18	52	3.96	5	42	1.66
7	3	51	(43-63)	8	61	4.47			
8	6	55	12.71	14	65	6.70	8	59	9.98
9	6	61	8.81	13	67	7.94			
10	7	58	12.48	11	78	11.58			
11	6	62	11.08	9	76	11.55			
12	6	69	15.51	8	84	11.76	8	72	8.92
13	3	73	(68-82)	10	91	16.65			
14	5	76	14.98	8	94	17.00			
15	6	77	16.11	6	90	11.29	8	83	6.98
16	2	81	(80-82)	4	94	3.69			
17				10	101	15.51			
18	4	92	16.11	4	95	8.26			
19	2	82	(75-89)	3	107	(104-111)	7	87	8.71
20				2	110	(108-113)			
21	4	95	5.62	5	109	9.00			
22				3	101	(93-110)			
23	4	94	5.86	6	105	9.02			
24	2	94	(89-99)	3	110	(107-112)			
25	3	102	(95-108)	4	109	13.52			
26				5	103	9.25			
27	4	102	7.28	4	108	17.36			

* Two males were involved in each sample
** Estimated in field animals (see text)
\+ Range given where 3 or less animals weighed.

and the 140g - 180g weight groups.

From the time that young animals first began to be caught in February through to the end of May, females of all weights were present in the population. During winter (June to August) there was a build up of animals less than a year old in the 86g - 110g weight class, and this was more marked in 1964 than in 1965. As these animals commenced to grow again in the spring (September, October) the numbers became more or less equally divided between the 86g - 110g and the 111g - 140g classes, and by the beginning of the breeding season again most females were in the 111g - 140g weight class.

Male numbers at the onset of the breeding season (November) were more or less equally divided between the 121g - 140g and the 141g - 180g classes, i.e., many were considerably heavier than the females at that time. During the peak breeding months (December and January) nearly all males were over 140g and many were in the 181g - 200g class, again many being much heavier than the females. From February to the end of May all weight groups became represented in the population, as they were with the females. During the winter there was a marked tendency for the males to weigh between either 86g - 120g or 141g - 180g. The animals in the former weight class were mainly maturing young while the latter were older animals passing through their second winter. In September and October body weight began to increase, and animals approaching their first breeding season began to move into the 121g - 140g weight class, and by November most animals weighed more than 120g.

(iii) Discussion

The growth curve of R. fuscipes was in agreement with the findings of Warneke (1964) for the species in Victoria. He found that females tended to grow more slowly than males, but thought his method of ageing

animals on incisor width may have caused his result. However, as he pointed out, Taylor (1961) also got slight differences between male and female growth in a laboratory colony. It seemed therefore that there was a certain degree of sexual difference in body weight, and this was supported by the monthly distribution of weight classes for field animals where, in every month, the highest weight class in which females were common was always one class below the top class in which males were common. Though there was no evidence that these females and males were all the same age, there was evidence that the female survival rate was higher than that of males (section VIII). Therefore, if anything, the females were older than the males. Thus it can be assumed the weight difference was real, and not due to the males being older than the females.

A check to growth at about five months was recorded by Warneke (1964) who noted that this corresponded to the winter period in the field. The cessation of growth in Mt. Glorious animals shown in the growth curve coincided with the winter months, and in the field all animals stopped growing in the winter, as was shown by the stabilisation of numbers within the different weight classes during June, July. In the spring a shift in numbers from the lower to the higher weight classes reflected the renewal of growth after the winter lull.

The less marked build up of numbers in the 86g - 110g and lower weight classes of the females during the winter months in 1965 compared with 1964, was due to the presence of more breeding adults in the population during the winter of 1965. The weight distributions of the males did not show a similar difference between the two years, since similar numbers of adult males were present in the population in both years.

The pattern of growth in which overwintering animals, which were mainly the young from the previous breeding season, remained at a lower weight than attained at full maturity, was typical of small mammals of temperate regions, as recorded for Microtus agrestis by Baker and Ranson (1933) and Clethrionomys glareolus by Jewell (1966a). In tropical regions small mammals grow throughout the year without a seasonal plateau in their growth curves, as has been recorded by Harrison (1955) for several species of Rattus in Malaya, and by McDougall (1946a) for R. conatus in northern Queensland. It seems unclear as to whether a lull in growth during winter is a direct effect of a drop in food supply, as suggested by Shillito (1963a), or whether it is an adaptation which allows the maximum number of individuals to be carried through the winter, when their smaller size will minimise their food requirements at a time when food is scarce, as suggested by Jewell (1966a).

(iv) Weight as a criterion of age

In order that a better understanding of population changes and movement patterns may be gained, it is necessary to have relative age information on the individuals involved, and body weight has been used to define three age groups in R. fuscipes - juveniles, sub-adults, and adults. These body weights and their biological implications are discussed below.

In R. fuscipes at Mt. Glorious, perforation of the vagina had occurred in practically all animals before their first capture, and was therefore of no value as a criterion of the determination of juvenile animals. To ascertain a suitable weight on which to classify juveniles, data from the laboratory colony studied by Taylor (1961) was used in conjunction with the growth curve of field animals at Mt. Glorious. Taylor found that females less than 50 days old had

not begun to ovulate, regardless of whether their vagina was perforate or not. Ovulation usually began in the third month at which time the vaginal smear pattern stabilized to a series of regular cycles. Further, the young males in the colony did not start to mature sexually until about $2\frac{1}{2}$ months old. Thus the young of this species were reproductively immature under 50 days old. From the growth curve (Fig. 4) the mean weight at this age of males was 61g and of females 51g, and these weights were used to delimit the juvenile age class. Though some animals born late in the breeding season were still in the juvenile weight range in what was known to be their third month, such animals were few. Similarly a few extremely rapidly growing animals overshot the weight limit while apparently under 50 days old, but on the whole the weight limits appeared to be meaningful and useful.

As the juveniles grew they became classed as sub-adults. The upper limit of this age group was delimited by the maximum weight reached by the young animals at the time of the winter lull in growth, i.e. 110g for females and 120g for males. Few animals exceeded these weights before their first winter, and few having once passed them to become adults fell below them again. As can be seen in Figures 5 and 6 many animals of both sexes remain in this weight category well into the spring, so that the upper age limit of the class may be quite variable. However, the animals falling into the class formed a biologically significant group, namely, animals which usually did not breed though they had reached puberty, and were therefore potentially capable of breeding. Females over 110g and males over 120g were classified as adults.

Thus for R. fuscipes in this study juvenile refers to males 60g or less, females 50g or less: sub-adult refers to males 61g - 120g, females 51g - 110g, and adult to males above 120g or females above 110g.

B. Melomys cervinipes

(i) Results and Discussion

There were insufficient data to plot a growth curve or construct a diagram of the monthly body weight distribution for this species.

Adult animals were considerably smaller than R. fuscipes, only 24 animals attaining a body weight of more than 90g. The maximum weight recorded for an individual was 103g for an old male animal, but generally there was no difference in body weight between the sexes.

Out of the 111 animals caught during the study only 24 weighed less than 60g at their first capture, and only 10 weighed less than 40g. Thus most of the animals captured had a body weight within the range of 60g - 90g.

Since many known adult adimals weighed only 60g - 70g, it was often difficult to distinguish sub-adults from adults. Further, in females that had stopped breeding the vagina became imperforate, as it was in younger animals before they commenced to breed, and known adult males were recorded with abdominal testes. However females under 65g at their first capture, and which were imperforate and had very small nipples, were classed as sub-adults, as also were males of similar weight with abdominal testes.

No seasonal weight changes were distinguishable from the data.

C. Antechinus stuartii

(i) Methods

In this species there were no problems in ageing individuals, since the well synchronised breeding of all females in the population resulted in each year's young animals all being the same age to within about two weeks. Further, no second year males occurred in the population, and second year females were readily identified from the condition of their

Table 3. Monthly mean weights of female Antechinus stuartii in grammes.
(N = sample size, M = mean weight to the nearest gramme, S = standard deviation).

	1963-1964			1964-1965			1965-1966			1966		
	N	M	S	N	M	S	N	M	S	N	M	S
Feb. 1st - 10th				2	15	(13,17)+	9	16	1.33	1	13	-
Feb. 11th - 28th				0	-	-	0	-	-	0	-	-
March				4	23	2.24	10	21	1.86	8	21	1.19
April				9	24	2.18	22	24	1.85	8	23	1.07
May				12	23	2.20	32	23	1.41	3	24	1.73
June				18	22	1.51	40	23	1.52	11	24	1.87
July				15	22	1.61	31	23	1.81	3	23	1.00
August				17	22	1.97	19	24	1.47	2	26	(25,27)
September	11	27	3.14	15	28	2.36	18	28	1.60	6	30	0.78
Oct. 1st - 21st*	8	25	3.12	11	27	2.43	13	28	1.92	0	-	-
Oct. 22nd - 31st*	9	29	2.74	12	31	3.06	13	32	2.20	0	-	-
November	9	33	3.76	15	36	3.26	10	36	4.39	0	-	-
December	6	32	1.95	11	34	3.39	13	33	1.66	5	36	2.18
January	3	30	0.57	15	36	2.79	13	35	2.88			
February**	5	31	2.13	16	34	3.38	9	32	1.73			
March	2	32	(30,34)	26	33	2.25	4	32	0.87			
April	2	32	(31,33)	19	34	2.45	1	32	-			
May	2	28	(27,29)	28	34	3.27	1	29	-			
June	2	28	(27,29)	36	30	2.02	4	35	1.73			
July	2	28	(27,29)	24	31	2.27	1	30	-			
August	2	27	(25,29)	12	31	1.68						
September	2	32	(31,33)	13	33	1.47						
Oct. 1st - 21st*	1	30	-	11	32	3.23						
Oct. 22nd - 31st*	1	31	-	8	37	3.40						
November	1	40	-	6	40	2.28						
December	1	34	-	6	37	2.61						
January				7	39	4.08						
February				5	36	3.28						

* October 1st - 21st animals pregnant, October 22nd - 31st animals carrying pouch young.

\+ Individual weights

** The division of February into two periods was only important for the fast growing recently weaned young

nipples. Consequently the growth curves (Fig. 7 and 8) for this species were obtained by averaging the weights of all animals of the relevant sex and year group captured in each month.

(ii) Results

From these average weights (Tables 3 and 4) it could be seen that males were larger than females in this species, from the time when the young first entered the traps in February at the age of 3½ months, to the time when the males died at the end of September.

Table 4 Monthly mean weights of male Antechinus stuartii in grammes. (N = sample size, M = mean weight to the nearest gramme, S = standard deviation).

	1963			1964			1965			1966		
	N	M	S	N	M	S	N	M	S	N	M	S
Feb. 1st - 10th				1	20	-	6	15	2.98	0	-	-
Feb. 11th - 28th				10	26	4.23	10	23	2.85	4	24	0.57
March				11	30	3.87	30	26	2.38	13	26	4.71
April				10	35	3.49	23	32	3.45	9	30	2.54
May				20	37	3.96	54	33	4.53	10	31	2.33
June				27	37	5.16	62	32	4.18	19	36	4.79
July				18	37	4.93	60	32	4.20	9	34	4.40
August				18	39	5.30	42	37	5.50	9	34	5.62
Sept. 1st - 16th*	6	62	10.44	28	51	6.63	46	46	5.51	12	50	5.21
Sept. 17th - 30th*	8	41	8.05	1	44	-	8	42	6.67	2	40	(36-44)+

* Sept. 1st - 16th premating period, about Sept. 17th onwards mating and post-mating period.

\+ Individual weights.

First year females grew from a weight of about 15g in early February to about 23g in May (Fig. 7). Through the winter, to the end of August, body weight remained relatively steady, then rose to about 29g at mating time (mid-September). During pregnancy and the period of pouch occupancy by the young, the weight of mother and young combined rose sharply to a peak of about 36g in November. After the young were deposited in the nest the mother's weight fell irregularly to about 30g.

Those adult females which lived on after weaning their first litter remained at about 30g to the end of their second winter, i.e. they overwintered at about 6g heavier than young females in their first winter. As the weight of young females rose during pregnancy and the period of pouch occupancy by the young, the weight of second year females consistently averaged four or five grammes heavier than that of the first year animals.

Until just prior to the mating season the pattern of male growth was similar to that of the females though their growth rate was greater (Fig. 8). When first caught at 3½ months old in February they were 5g - 10g heavier than the females. The disparity between the weights of the sexes continued to increase, and by late autumn (May) the males were 10g to 15g heavier than the females. During the winter months of June and July, growth ceased as it did in the females. From August to mid-September male body weight rose sharply by 10g - 15g, though female body weight only increased by about 5g during the same period. Mating occurred from mid-September onwards, and, while female weights continued to rise, the weights of those males which survived to the end of September fell by up to 10g, and one individual lost 19g.

(iii) Discussion

Sexual dimorphism in body size was noted by Horner and Taylor (1959) from body measurements of museum specimens. They also noted that the disparity in size was in the opposite direction to the tendency suggested by Jones (1923), that the females usually exceeded the males in size in the few examples which occurred among carnivorous marsupials. Horner and Taylor also state (p. 22) "Any possible selective advantage of such sexual dimorphism must remain, of course, purely speculative at present."

It seems probable that male size was selectively favoured along with male aggressiveness which was discussed in the previous section.

Woolley (1966) has followed body weight changes in the laboratory of A. stuartii from southern New South Wales. Though her data on weight changes during the breeding season, particularly of the females, was more detailed than was recorded at Mt. Glorious, the basic pattern of the changes was the same. She found that the male body weights rose sharply by about 10g prior to mating and then fell again as in the field at Mt. Glorious. Female weights, and post-partum female plus pouch young weights, increased during the period from one week before mating to the end of pouch occupancy by the young, as was recorded at Mt. Glorious. However, her more frequent weighings during pregnancy showed a sharp rise in female weight in the last 5 - 10 days of the gestation period, followed by an equal drop in weight at birth. These changes were not recorded at Mt. Glorious.

Though female weights in the three study years at Mt. Glorious were similar in each year, there were considerable differences in the average weights of males between years, particularly during the breeding season. In 1963 the average weight of the males trapped in early September was 62g compared with 51g in 1964, 46g in 1965 and 50g in 1966. Since female weights between these years did not vary appreciably the cause of the male differences was not clear. In 1963, when the male weights prior to breeding were extremely high, the previous history of the animals was unknown. However, comparing 1965, when the lowest weights at mating time were recorded, with 1964 and 1966, it was seen that the body weights of males throughout the winter months also were markedly lower in 1965 than in 1964 and 1966 (Fig. 8). It seemed, therefore, that 1965 was a poor year for males throughout, and in fact in 1965 Queensland experienced a drought year.

The average rainfall from January to June dropped from 40 inches in each of the three preceding years to 17 inches in 1965 at Mt. Glorious.

These dry conditions could be expected to have detrimentally affected the forest litter fauna, one source of food for this insectivorous species. However, such a bad year would also be expected to affect female weights and they were unchanged. There was one piece of evidence to support the suggestion that the dry conditions were having an effect on males. In August 1965, following rain in July, (Fig. 2), male weights rose appreciably, and such a rise was not recorded in 1964 and 1966, nor in the case of females in 1965 (Fig. 8).

The pattern of growth incorporating a winter lull was similar to that of R. fuscipes, and, as previously noted, typical of temperate and not tropical regions. The rapid increase in weight of males at the breeding season could be compared with that of a eutherian insectivore such as Sorex araneus which have a burst of growth during the month prior to breeding. Females of A. stuartii however did not show this prebreeding increase in growth to the extent that the males did, though it was the females which would have the burden of rearing the young. However, in A. stuartii, both the gestation period and lactation are long so that the demands on the female would not be so great as in the case of S. araneus (gestation about 15 days: lactation 21 days: 2 - 5 litters per year) (Southern 1964) in which the weight in sexually maturing females almost doubles during the two months prior to breeding (Shillito 1963a).

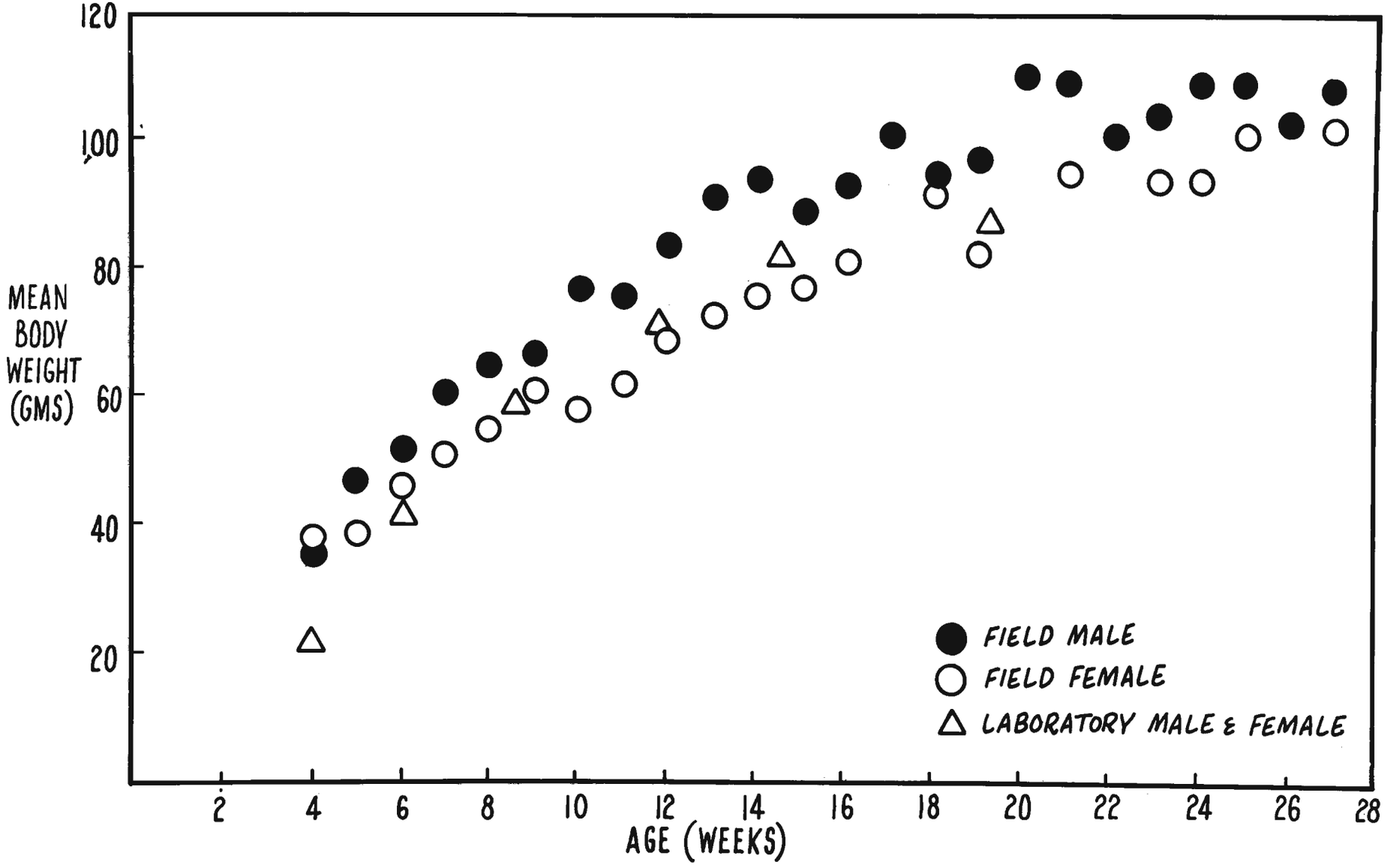


FIG. 4 MALE & FEMALE R.FUSCIPES GROWTH CURVES FROM FIELD & LABORATORY BODY WEIGHT DATA IN TABLE 2.

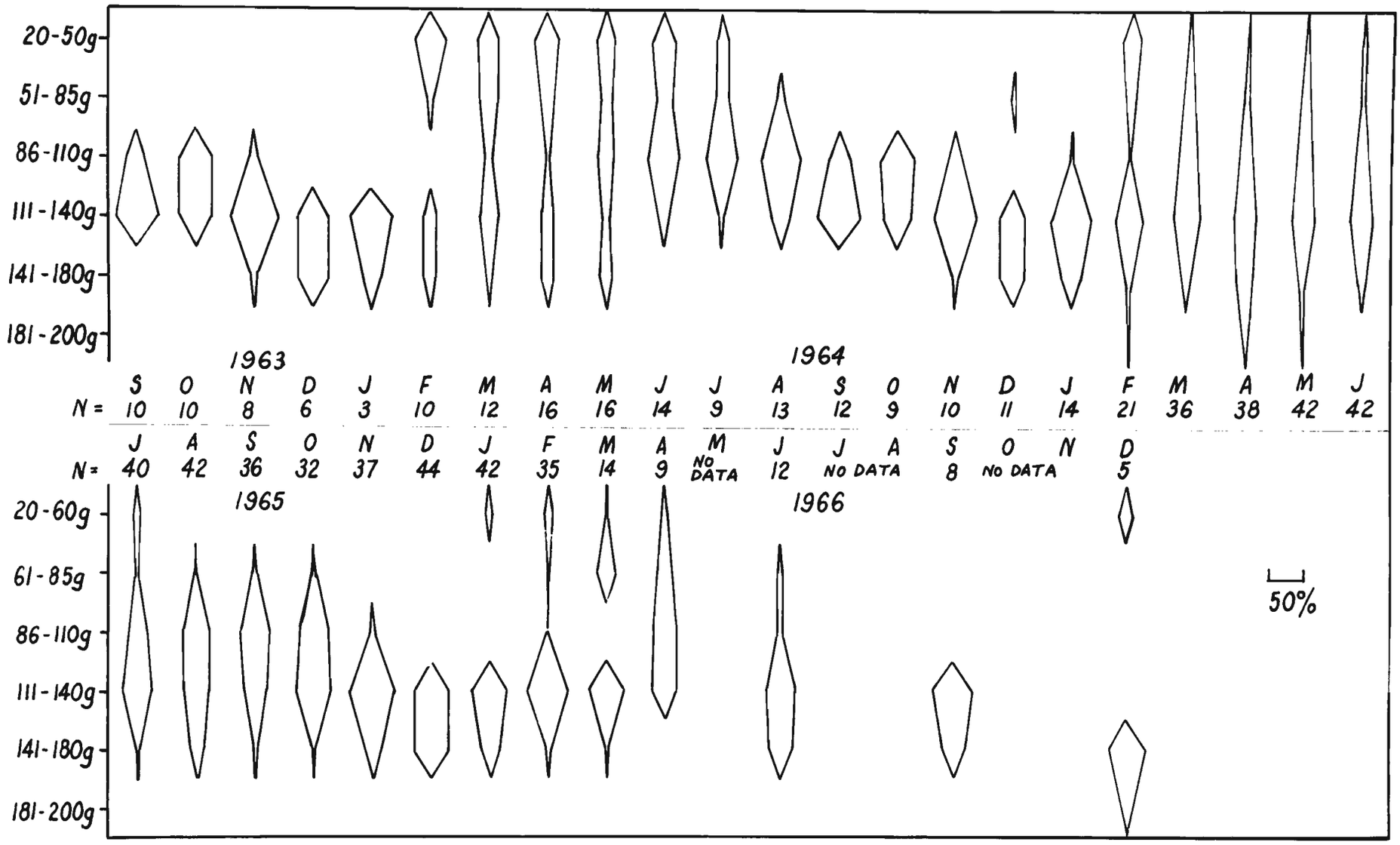


FIG. 5 MONTHLY BODY WEIGHT DISTRIBUTION OF R. FUSCIPES FEMALES (N = SAMPLE NUMBER).

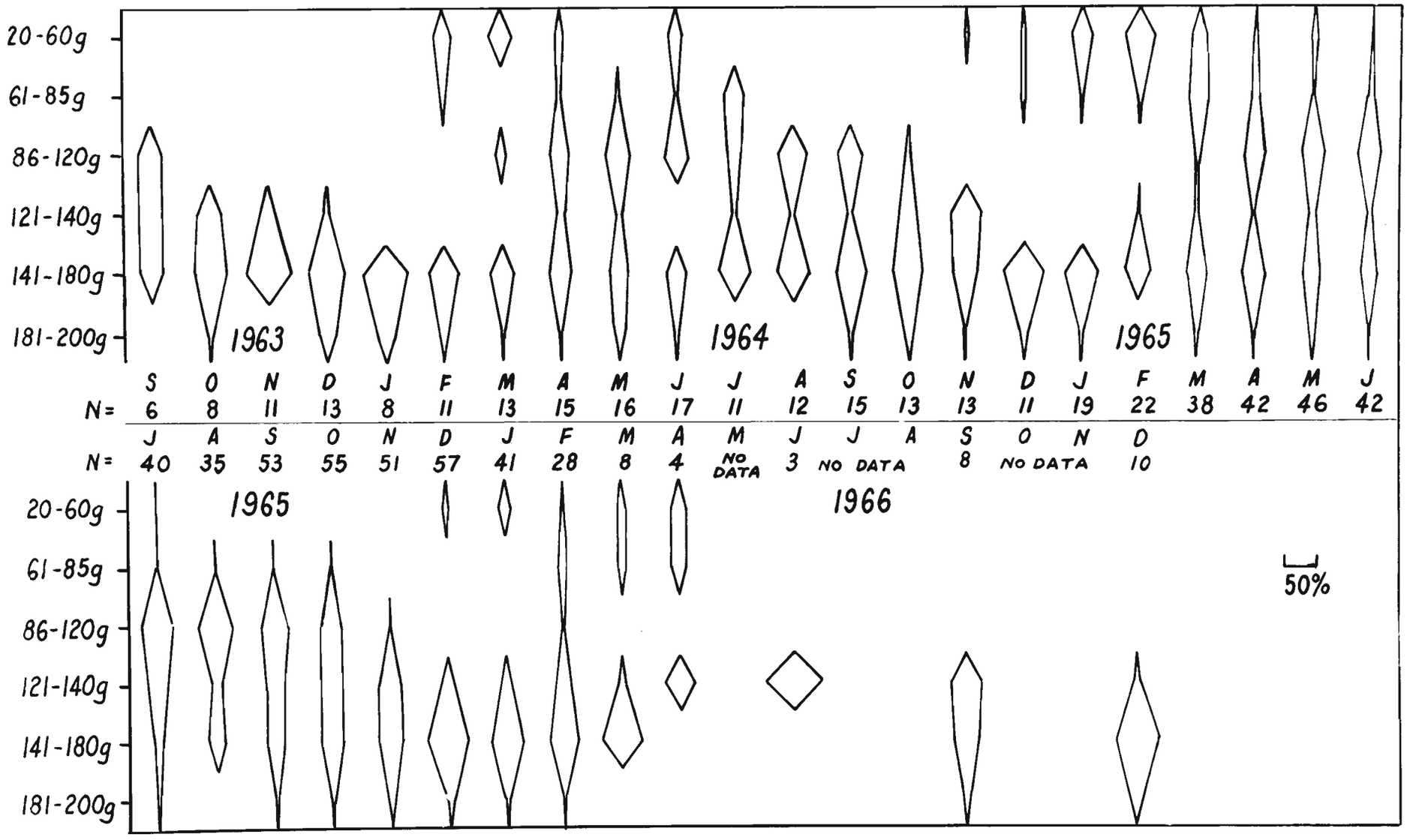


FIG. 6 MONTHLY BODY WEIGHT DISTRIBUTION OF R. FUSCIPES MALES (N= SAMPLE NUMBER).

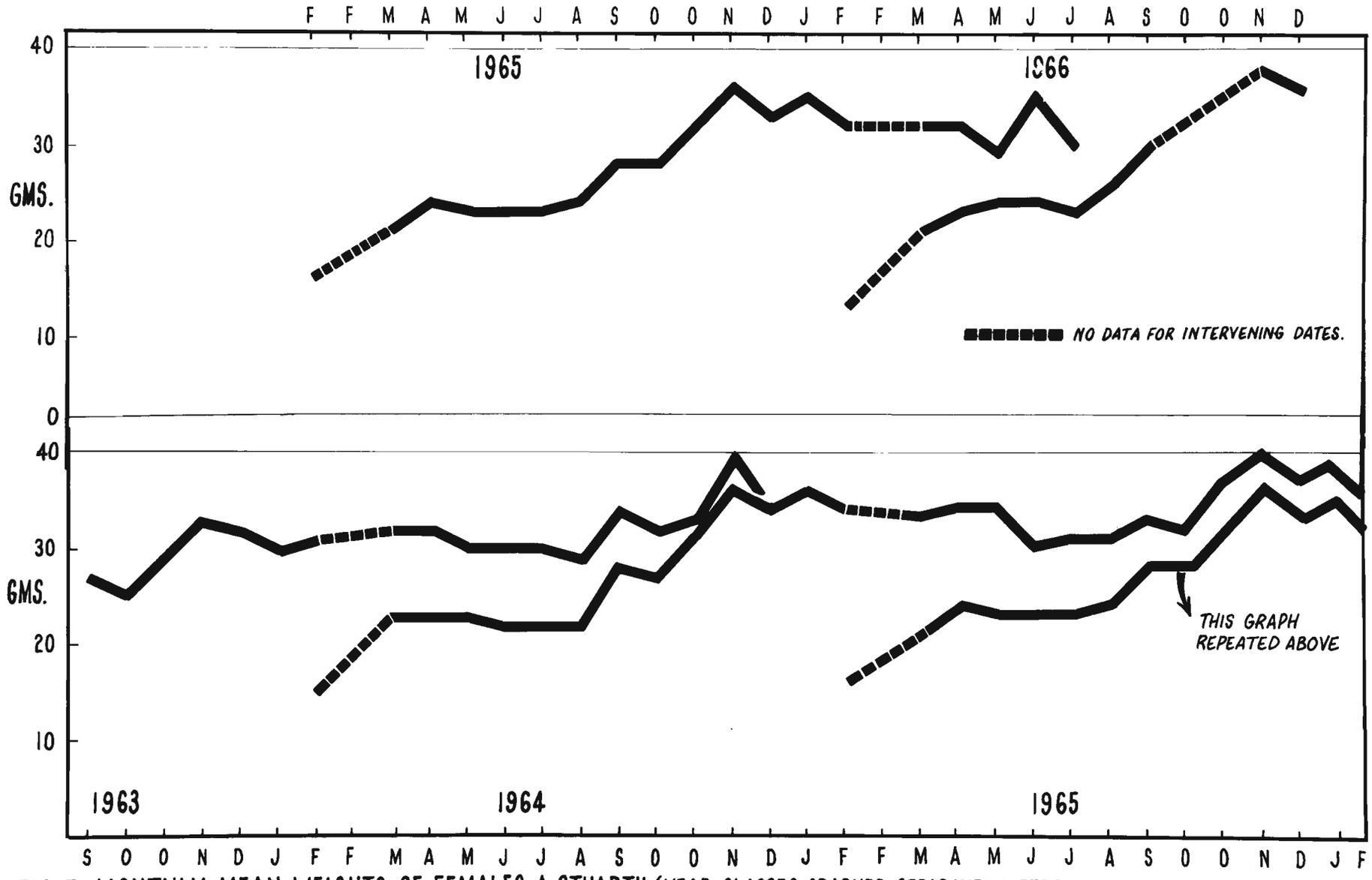


FIG. 7 MONTHLY MEAN WEIGHTS OF FEMALES A.STUARTII (YEAR CLASSES GRAPHED SEPARATELY; FEBRUARY AND OCTOBER BIMONTHLY WEIGHTS PRESENTED, SEE TABLE 3).

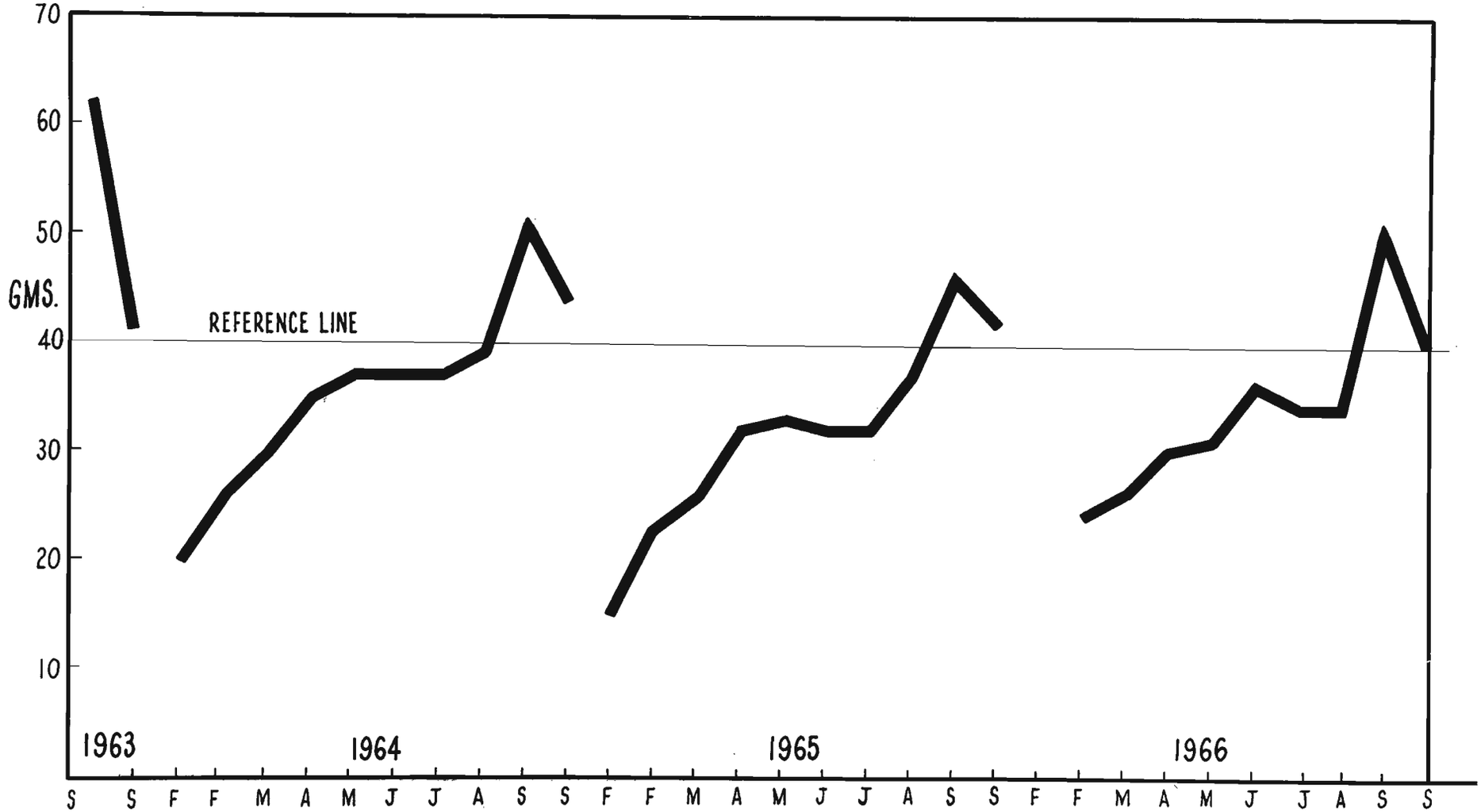


FIG. 8 MONTHLY MEAN WEIGHTS OF MALE A. STUARTII (FEBRUARY AND SEPTEMBER BIMONTHLY WEIGHTS PRESENTED, SEE TABLE 4)

VII HOME RANGE AND MOVEMENT PATTERNS

A. Methods

(i) Home Range

It has been recognised for some time that the maximum distance between captures continually increases for an animal which repeatedly moves into new areas, but for an animal which occupies a home range with more or less fixed boundaries, the maximum distance between captures will stop increasing after a certain number of captures. At this point it can be assumed that the animal has been captured near to the extremities of its range (Stickel 1954). The average maximum distance between captures, i.e. average observed range length (Av. O.R.L.), was used as an index of size to compare the differences in home range between the species studied.

In order to determine the number of times an animal must be captured before it can be assumed that it has been caught near to the limits of its range, a plot was made of the length of the average maximum distance between capture points after the second, third, etc. captures (along the ordinate) against the number of captures (along the abscissa) (Figs. 14 and 15). If animals were finally caught at the extremities of their range, this curve should level off parallel to the abscissa, and the number of captures required to reach this point can be read off. Only animals with such a number of captures or more were used for the calculation of the average O.R.L.

The average O.R.L. was calculated twice for each species and for each sex, once from grid captures only, and once from line captures only. Many animals that had home ranges which only impinged on the grid by 50 ft. (15.25m) (i.e. to the second trap row) and would therefore have given misleadingly small O.R.Ls., were excluded from the 'grid' calculations. Also, captures which were considered to be the result of dispersal movements were excluded from the calculations of the O.R.Ls., and known home range shifts were also corrected for. Two examples of dispersal movements are given for R. fuscipes in Figure 9. In both cases the animals were adults. ♀ 5887 and ♂ 5481 were each caught at a point well separated in space and time from the rest of the captures for each animal, thus indicating that they were no longer using the area in which they were first captured. Such captures were not included in the measurements of O.R.Ls. However similar "space isolated" captures, if preceded and followed by captures within the central area of the home range of an animal, were considered to indicate "exploratory sallies", and were included in O.R.L. calculations. This concept of home range was as defined by Jewell (1966b, p. 1o3) - "home range is the area over which an animal normally travels in pursuit of its activities," and differed from the usually accepted definition of home range by Burt (1943) mainly by the inclusion of "exploratory sallies", which were specifically excluded by Burt.

Jewell (1966b) considered "exploratory sallies" as being important since by such movements animals maintained or expanded their home ranges. Since the adult males of both R. fuscipes and A. stuartii were wide ranging, the former being prone to shifting their home range, and the latter tending to continually expand their home range (see below), Jewell's concept of home range seemed particularly relevant to these species.

The grid was too small in the case of the males of R. fuscipes and A. stuartii to enable a meaningful calculation of an average home range area to be made, since most of the animals which were captured a sufficient number of times had ranges which considerably overlapped the edge of the grid. However, range areas for the few female animals of these species,and all M. cervinipes with sufficient recapture records and relatively few captures in the edge traps of the grid, were calculated by the exclusive boundary strip method (Stickel 1954). Where animals were caught in edge traps, a strip 25 ft. (7.6m) wide was added to the area.

(ii) Movement patterns

Movement patterns - 'actual movements in three-dimensional space that an animal makes during any specified period of time' (Brant 1962, p. 125), were investigated by an analysis of the distance between consecutive captures (D ft.) Many workers have used between capture distances for assessing movements of small mammals, as noted by Brown (1962). Brant (1962) showed the usefulness of the measure as an index of movement patterns for comparative purposes between species and seasons. Average D values were therefore calculated for appropriate periods of time and classes of animals.

Since distance between traps will obviously affect the calculated value of average D, and since comparisons were being made between seasons in which some of the trap spacings varied from the regular grid spacing of 50 ft. (15.25m) (i.e. trap ring operated April - November with traps 100 ft. (30.5m) apart, line trapping operated March 1965 - February 1966 with trap stations 200 ft. (61m) apart), only captures in the grid set of traps have been used. Any other captures of an animal have been ignored.

The length of time between recaptures also will have an important influence on the average D values. Therefore only recaptures which were

two weeks or less apart have been used.

Some animals were noted to have shifted their home range between recaptures, and allowance was made for these cases in the calculations. Aberrantly long recapture distances might also have been recorded as transient individuals passed through the grid, though it was more likely that such animals would be caught only once on the grid and so provide no data toward the calculation of average D. However recaptures of transients have been ignored.

A circumstance in which too short distances might have been recorded was that of an animal whose home range impinged on one or two edge traps of the grid only. All captures of such an animal were likely to have been in the same or neighbouring edge traps. From the trapping results it was apparent that this occurred relatively frequently and would have provided sufficient aberrantly small distances to markedly affect the average D values. Consequently animals caught only in edge traps have not been used in calculations of average D.

B. Home Range

(i) Results

Trapping indicated that all three species occupied home ranges and some examples are given in Figures 9, 10 and 11. Home ranges of both males and females overlapped considerably (Figs. 12 and 13) in both R. fuscipes and A. stuartii. Individual male ranges overlapped several female ranges. There were insufficient data to map home ranges for M. cervinipes.

Analysis of the maximum distance between captures on the grid showed that in R. fuscipes (Fig. 14c) the distance stopped increasing after fifteen captures for males and seventeen captures for females. The curve for the males showed a rise between the twenty third and twenty sixth captures, but this was due to loss from the samples of animals with small

maximum distances between captures. Over this period N dropped from 12 to 5 (Table 5). Where N remained constant after the fifteenth capture, the maximum distance between captures also remained constant. Therefore the average O.R.L. was calculated for R. fuscipes from males with 15 or more captures and females with 17 or more captures. For the males of N. cervinipes the maximum distance between captures increased steadily to the tenth capture. Fluctuations in the curve after this point were mainly the result of loss of animals from the sample, though the maximum distance between captures of one animal increased slightly between the eleventh and twelfth captures. The maximum distance between captures in the case of females ceased to increase after the twelfth capture (Fig. 14b) except for one animal which continued to be caught at more distant traps up to the twenty second capture. Other irregularities in the curve past the twelfth capture were due to changes in the sample size as in the case of males (Table 5). Thus the average O.R.L. was obtained by using male animals with 10 or more captures and females with 12 or more captures.

The graphs for the males and females of A. stuartii however did not level off (Fig. 14a), though that of the females rose very much more slowly after the sixteenth capture - maximum distance between captures increased only 25 ft. (7.6m) between the 16th and 30th capture compared with 109 ft. (33.25m) between the second and the sixteenth capture. So for practical purposes it was assumed that after 16 captures, females of A. stuartii had been captured at about the extremities of their ranges, and the O.R.L. was calculated from these animals. Though the curve for the males did not level off, it could be seen that, after the fifteenth capture, where the sample size remained constant the maximum distance between captures did not increase (Table 5). All the increases resulted from animals with small values for their maximum distance between captures

Table 5 Average observed range length in feet (Av. O.R.L.) at consecutive captures for R. fuscipes, M. cervinipes and A. stuartii from "grid trapping" data. (N = sample size).

	R. fuscipes				M. cervinipes				A. stuartii			
Number of	♀		♂		♀		♂		♀		♂	
Captures	N	Av. ORL	N	Av. ORL	N	Av. ORL	N	Av. ORL	N	Av. ORL	N	Av. ORL
2	25	80	53	111	35	52	23	67	29	79	41	73
3	24	106	50	154	23	65	16	86	24	95	35	99
4	24	124	43	177	16	77	12	97	22	123	31	116
5	22	142	39	205	12	84	9	107	20	128	31	135
6	22	148	36	218	8	115	6	122	20	134	27	141
7	19	151	32	223	6	92	6	129	19	144	23	156
8	17	166	28	227	6	92	6	144	18	151	21	177
9	15	171	28	229	6	117	6	152	17	157	19	183
10	14	178	23	230	5	117	6	174	16	150	17	188
11	14	182	21	237	4	126	3	165	15	151	16	186
12	14	185	20	241	4	130	3	175	15	151	16	197
13	13	179	20	241	4	130	2	191	14	176	14	207
14	13	179	19	246	3	114	1	158	13	180	11	223
15	13	186	18	264	3	114	1	158	12	182	10	229
16	12	191	17	263	3	114	1	158	11	188	9	226
17	12	195	16	259	2	92			10	172	8	232
18	11	196	14	262	2	92			9	174	8	232
19	11	196	13	262	2	92			8	170	6	239
20	11	196	13	262	2	126			8	189	4	255
21	10	197	13	273	2	146			8	191	4	255
22	9	196	12	264	2	146			8	191	3	257
23	8	198	12	264	2	146			8	197	2	314
24	7	191	9	280	2	146			8	197	2	314
25	7	196	7	290	2	146			8	197	2	314
26	7	196	5	304	2	146			8	200	1	403
27	7	196	4	305	2	146			7	206	1	403
28	7	202	3	300	2	146			6	208	1	403
29	7	202	3	300	2	146			6	213	1	403
30			2	248	2	146			6	213		
31			2	248	2	146			6	213		
32			2	248	2	146						
33			2	248	2	146						
34					2	146						
35					2	146						
36					2	146						
37					2	146						

dropping out from the samples. Thus for the calculation of the average O.R.L., it was assumed that the maximum distance between captures for individuals did not increase appreciably after 15 captures. That this assumption was not entirely valid was shown in the analysis of the line trapping data below.

During the "line trapping" programme all individuals of M. cervinipes except one were recaptured only at the same trap site. Trap sites were obviously too far apart to measure the O.R.L. for this species.

The graphs of the maximum distance between captures from "line trapping" for both males and females of R. fuscipes showed a steady increase in the maximum distance between captures followed by large fluctuations (Fig. 15a). In the females the fluctuations commenced after the tenth capture and were mainly due to loss of individuals with small values from the samples. Where N remained constant the maximum distance between captures did also (Table 6). The steady increase in the maximum distance between captures in the males ceased after the twelfth capture and the curve became very irregular. These irregularities were partly the result of individuals dropping out of the samples, and partly due to actual increases in the maximum distance between captures of six of the ten individuals captured more than ten times. Therefore, though an average O.R.L. for males was calculated from animals with twelve or more captures, the estimate seemed very likely to be low, as many animals may not have been caught at the extremities of their ranges even after 12 or more captures.

The maximum distance between "line" captures for females of A. stuartii (Fig. 15b) increased steadily to the sixth capture and then commenced to fluctuate with changes in the sample number. Only one animal showed an increase in the maximum distance between captures after the sixth capture. However in the case of the males (Fig. 15b) the graph rose steeply to the

Table 6 Average observed range lengths in feet (Av. O.R.L.) at consecutive captures for R. fuscipes and A. stuartii from "line trapping" data. (N = sample size).

	Rattus fuscipes				Antechinus stuartii			
	♀		♂		♀		♂	
Capture	N	Av. ORL	N	Av. ORL	N	Av. ORL	N	Av. ORL
2	65	60	79	195	73	43	75	119
3	50	115	56	241	48	120	55	165
4	42	151	43	297	40	154	40	288
5	35	164	36	373	32	173	27	385
6	33	171	34	390	22	198	22	416
7	26	201	26	406	16	172	17	416
8	25	241	20	455	12	163	14	359
9	21	277	15	482	9	181	11	381
10	18	289	12	534	7	232	7	400
11	16	239	10	561	6	238	6	467
12	13	279	10	620	4	257	4	550
13	12	345	9	560	3	200	2	563
14	11	340	9	560	1	200	2	663
15	8	361	8	622	1	200	1	925
16	7	384	8	622			1	925
17	5	417	5	506			1	1055
18	3	327	5	590			1	1055
19	3	327	4	538				
20	3	327	2	645				
21	3	327	2	645				
22	3	327	1	912				
23	3	327						
24	2	200						
25	1	200						

fifth capture, levelled off between the fifth and seventh captures, and commenced rising very steeply again to the fifteenth capture. The drop between the seventh and eighth captures was due to the disappearance from the samples of an animal with a large maximum distance between captures. Since many of the animals were caught repeatedly throughout their full life span, it appeared that they continually expanded their home range throughout life, and particularly in September (see Fig. 11). However, since the maximum distance between captures had a tendency to level off between the fifth and seventh captures, an average O.R.L. was calculated for animals with 7 or more captures. This O.R.L. for males of A. stuartii can only be used as a broad index to the size of their home range, useful only for very general comparisons, and can almost certainly be considered an underestimate of their "lifetime" home range.

Average O.R.Ls. from "grid trapping" and "line trapping" are given in Table 7.

Home range areas were calculated from the "grid trapping" results for three females of both R. fuscipes and A. stuartii and two females of M. cervinipes. All animals had 30 to 40 capture records. In the case of R. fuscipes as many as one third of the captures were in traps on the edge of the grid but in the case of M. cervinipes and A. stuartii less than one sixth of the captures were in edge traps. It was likely therefore that all ranges were underestimates, particularly those for R. fuscipes. No attempt was made to calculate range sizes for male animals since insufficient captures were recorded for M. cervinipes, and males of R. fuscipes and A. stuartii had ranges larger than two acres, the size of the grid (see discussion below). Ranges for female R. fuscipes were 1.06, 1.08 and 1.45 acres (0.43, 0.44 and 0.59 ha); for M. cervinipes 0.34 and 0.45 acres (0.14 and 0.18 ha); and for A. stuartii 0.80, 0.98

and 1.15 acres (0.33, 0.39 and 0.46 ha).

(ii) Discussion

In both R. fuscipes and A. stuartii the average home range of the males was considerably larger when calculated from the "line trapping" data than when calculated from the "grid trapping" data (Table 7). The values of 736 ft. (224.5m) and 551 ft. (168m) for the O.R.Ls. calculated from "line trapping" of R. fuscipes and A. stuartii respectively showed that the grid, which measured 350 ft by 250ft. (106.75 by 76.25m), was too small to measure the ranges of these male animals. In the case of the females the "grid trapping" showed that the O.R.Ls. of both species were the same; however line "trapping data", while confirming the size of the O.R.L. of A. stuartii (about 200 ft. (61m)), gave considerably larger O.R.L. (over 300 ft. (91.5m)) for R. fuscipes (Table 7). Since one third or more of the grid captures of each of the females of R. fuscipes from which the average O.R.L. was calculated were in edge traps it seemed that the O.R.L. of R. fuscipes calculated from "grid trapping" was too small, and that the larger value calculated from "line trapping" was more accurate.

Table 7 Average observed range length (Av. O.R.L.) for R. fuscipes, M. cervinipes, and A. stuartii from "grid trapping" and "line trapping" data (N = sample size).

	R. fuscipes				M. cervinipes				A. stuartii			
	♀		♂		♀		♂		♀		♂	
	N	Av. ORL	N	Av. ORL	N	Av. ORL	N	Av. ORL	N	Av. ORL	N	Av. ORL
Grid data	12	218	18	293	4	168	6	179	11	219	9	253
Lines data	18	328	10	736	0	-	0	-	22	208	7	551

Thus the home range of R. fuscipes was somewhat larger than that of A. stuartii for the respective sexes, and in both species males had

considerably larger ranges than females.

The average home range of M. cervinipes was smaller than that of either R. fuscipes or A. stuartii (Table 7). There was little difference in size between the male and female ranges in M. cervinipes. The comparatively small size of their home ranges, which was obtained from "grid trapping" data, was supported by the "line trapping" results, where only one animal was recaptured at more than one trapping station i.e. in traps 200 ft. (61m) apart. It seemed therefore that their home ranges rarely extended this distance on the ground.

In general home range size is broadly related to body size by way of the maximum area that can be covered by an individual of a particular size, and more especially through the food requirements necessary to meet the different energy requirements of animals of various sizes (Jewell 1966b, McNab 1963). A further important factor in relation to energy requirements which affects home range size is type of food, i.e. whether animals are "hunters" (grain, fruit, insect or meat eaters) which have large ranges, or "croppers" (grass eaters and browsers) which have by comparison small ranges (McNab 1963). Many other factors modify home range size such as population density (Stickel 1960; Brant 1962), quality of habitat with respect to food and shelter (Blair 1943), the use made of the vertical dimension of the habitat (Benton 1955), and sex and social status (Brown 1966).

In this study there was not sufficient data to compare home range size with differences in population density, and the quality of the habitat was not studied intensively. The use made of the vertical dimension of the habitat though was investigated (Section X), and the results were used in comparing the home range size of the three species,

but social status of individuals was unknown.

However the comparison between the range size of each of the three species studied seemed to be best understood in the light of the general relationships suggested by McNab (1963). A. stuartii was clearly a "hunter", being entirely insectivorous (Wakefield and Warneke 1967). R. fuscipes was about 50% insectivorous taking also some fruit, seeds and other vegetable matter (Harrison 1961) and therefore falls halfway between "cropper" and "hunter". M. cervinipes was mainly a "cropper", stomachs containing about 80% leaf, shoot and vegetable matter, 15% fruits and 5% insect material (Harrison 1961). Personal observations on a few individuals from Mt. Glorious of each species confirmed the above findings.

If the results from the line trapping were taken as the better estimates of the range size for both sexes of R. fuscipes and for the males of A. stuartii, and a reasonable estimate for the females of A. stuartii, a comparison between the respective sexes of these two species showed that the home range of R. fuscipes was about one and a half times that of A. stuartii. However, the discrepancy in size was not as great as might have been expected in view of the difference in body size, (R. fuscipes was about four times the weight of A. stuartii), and the fact that A. stuartii had a large vertical component to its range which would be expected to further reduce the area of the forest floor it used. As pointed out above though A. stuartii was a pure "hunter", which class of animals have a range requirement about four times that of a "cropper" of equal body size (McNab 1963), or perhaps two to three times that of an animal with a mixed diet such as R. fuscipes. Therefore the comparative sizes of the home ranges of these two species was about what might be expected, when the interaction of the type of diet as well as body weight and habitat utilisation were taken into account.

From similar considerations it was not surprising that M. cervinipes had a much smaller home range than R. fuscipes. M. cervinipes was only about one half the body size of R. fuscipes, and was semi-arboreal (see section X) in marked contrast to R. fuscipes, individuals of this species rarely leaving the forest floor. Also M. cervinipes was a "cropper" compared with the half-way position of R. fuscipes between "cropper" and "hunter". All these factors suggest M. cervinipes would have a smaller range size than R. fuscipes.

However the smaller range size of M. cervinipes compared with A. stuartii was somewhat less expected, since both species were to a large extent arboreal so that no difference in range size would be expected from this factor. Further, M. cervinipes was at least twice the body size of A. stuartii, and would therefore be expected to have a larger not smaller home range. It seemed therefore that the observed difference between the size of the home ranges of these two species could only be understood from the type of food each utilises, M. cervinipes a "cropper" requiring less foraging space than A. stuartii a pure "hunter".

Though the home range data could not be satisfactorily analysed seasonally, the data on individual movements (see below) showed larger distances were covered by males particularly in R. fuscipes and A. stuartii in the breeding season than the non-breeding season, while the smaller distances covered by females varied little between the seasons. Since the average home ranges given in Table 7 were calculated from data collected over a period of six months or more for each individual, and therefore usually included the breeding season or part of it, the larger home ranges of the males of these two species compared with the females could be related mainly to the large movements of the males during the breeding season.

C. Movement patterns

(i) Results

The seasonal average D values are presented in table 8 for R. fuscipes and M. cervinipes. A comparison of these values for adults of R. fuscipes shows that male movements are significantly larger than those of females ($U = 2$, $n_1 = 5$, $n_2 = 5$, $P = 0.016$) - Mann - Whitney U test (Siegel, 1956). Female movements showed little variation between the seasons, but male movements were greater in the breeding season than the non-breeding season ($t = 3.36$, d.f. 188, $P < 0.05$ using Cochran's correction since F significant at 5% level (Snedecor 1956) for 1963/64 seasons; $t = 3.68$, d.f. 137, $P < 0.05$ using Cochran's correction, for 1964/65 seasons).

A comparison of the average D values for juvenile and sub-adults in the breeding season with those for the adults, showed that their movements were significantly smaller than those of the adults ($U = 9$, $n_1 = 6$, $n_2 = 12$ showing significance at the 1% level). A similar comparison of juveniles and sub-adults grouped together, with adults for breeding and non-breeding seasons grouped together, also showed that juvenile and sub-adult movements were significantly smaller than those of adults ($U = 21$, $n_1 = 10$, $n_2 = 16$, showing significance at the 0.1% level).

In M. cervinipes, though adult males generally showed larger movements than the females (Table 8), the samples were small and the difference was not statistically significant. Nor was there a significant difference between sub-adult and adult movements. No data were available for juvenile M. cervinipes.

Owing to the very different breeding behaviour of A. stuartii from R. fuscipes and M. cervinipes, which resulted in nearly all A. stuartii

Table 8 Average distance between consecutive captures in feet (Av. D) for R. fuscipes and M. cervinipes from "grid trapping" data. (N = sample size).

	Adults				Sub-adults				Juveniles			
	♀		♂		♀		♂		♀		♂	
	N	Av.D.	N	Av.D.	N	Av.D.	N	Av.D.	N	Av.D.	N	Av.D.
Season	R. fuscipes											
1963 - 64 Breeding	94	68	111	142	10	42	12	85	16	35	18	54
1964 Non-breeding	65	61	79	102	37	57	48	73	0		0	
1964 - 65 Breeding	129	69	54	121	18	25	42	56	16	52	36	60
1965 Non-breeding	117	65	85	67	18	51	110	58	0		0	
1965 - 66 Breeding	118	48	117	83	8	25	4	36	3	37	8	60
Average		62		103		48		62		43		58
Average both sexes		81				58				53		
	M. cervinipes											
1963 - 64 Breeding	14	61	3	91	0		0					
1964 Non-breeding	3	71	13	68	5	38	0					
1964 - 65 Breeding	35	43	20	92	6	71	4	83				
1965 Non-breeding	24	36	17	44	7	24	5	68				
1965- 66 Breeding	74	54	31	62	2	71	0					
Average		49		67		46		75				
Average both sexes		56				52						

individuals being the same age, the average D values were assembled in a different way. Each year was divided into one or two monthly periods and av. D calculated for each period (Table 9).

Table 9 Average distance between consecutive captures in feet (Av. D) for *A. stuartii* from "grid trapping" data (N = sample size).

	1963				1964			
	♀		♂		♀		♂	
	N	Av. D	N	Av. D	N	Av. D	N	Av. D
Mar. - Apr.	0	-	0	-	9	64	19	67
May - June	0	-	0	-	41	71	65	100
July - Aug.	0	-	0	-	48	62	61	95
Sept.	1	50	2	170	15	71	35	103
Oct. - Nov.	42	83	0	-	37	69	0	-
Dec. - Feb.	32	80	0	-	71	72	0	-
	1965				1966+			
Mar. - Apr.	14	53	57	70	27	62	42	73
May - June	27	53	53	96	48	68*	89	92*
July - Aug.	14	75	27	99	0	-	0	-
Sept.	7	83	3	152	20	83	60	118
Oct. - Nov.	13	98	0	-	0	-	0	-
Dec. - Feb.	21	105	0	-	10	73**	0	-

\+ Data from "activity trapping" programme used for 1966 results after April.

* June only.

** December only.

Throughout the period of March to September 1964 and 1965 male movements were significantly larger than those of females ($U = 2$, $n_1 = 4$, $n_2 = 4$, $P = 0.057$ for 1964 and for 1965) - Mann - Whitney U test (Siegel, 1956). During the early autumn (March - April), when the population consisted almost entirely of young animals 5 - 6 months old, male and female movements were much the same. During the late autumn and early winter (May - June) male movements increased significantly (F not significant at 5% level, $t = 2.75$, d.f. 82, $P < 0.01$ for 1964;

$t = 3.04$, d.f. 106, $P < 0.05$ using Cochran's correction since F significant at 5% level (Snedecor 1956) for 1965; and F not significant at 5% level , $t = 2.67$, d.f. 129, $P < 0.01$ for 1966), and reached their maximum in the breeding season (September). Though female movements had a tendency to increase through the winter and up to the mating season this was not significant. Male movements were much larger than those of females in the breeding seasons ($U = 0$, $n_1 = 4$, $n_2 = 4$, $P = 0.014$).

(ii) Discussion

In R. fuscipes the smaller movements of the juveniles and sub-adults compared with the adult, particularly in the breeding season, suggested that the pattern of behaviour of the young animals after weaning was to restrict their movements to around their natal home. Several multiple captures of an adult female with a young sub-adult supported this conclusion.

Dice and Howard (1951) have suggested that many of the young of small rodents disperse over relatively long distances, and Brown (1966) talks of the summer as "the time of dispersal of sub-adults and juveniles." This concept of dispersing young individuals did not fit the movement patterns in R. fuscipes. The line trapping programme furnished only two records of dispersion in young animals. Out of a combined total of 123 juvenile and sub-adults of R. fuscipes, marked during the line trapping programme, only one individual of each of these age groups was recaptured at locations which indicated that dispersion had taken place; i.e. one way moves from one group of capture points to another group of capture points. However 13 adult animals were recorded as having made dispersal movements (Table 10).

Table 10 Dispersal distances in feet and age distribution of all animals for which dispersal movements were recorded during the period in which the "line trapping" programme was carried out.

			R. fuscipes	
Distance (feet)	Adult		Sub-adult	Juvenile
	♀	♂		
601 - 800	1	2	0	1**
801 - 1000	3	3	0	0
1001 - 1200	0	3	1*	0
>1200	1	0	0	0
Total	13		1	1
			A. stuartii	
801 - 1000	0	1	0	0
1001 - 1200	1	0	0	0
>1200	0	1	0	0
Total	3		0	0

* female
** male

It was possible however that juveniles dispersed before they were first trapped. This could come about in two ways. Either they did not enter traps during the first two or three weeks of the post-weaning period, or the trapping interval was long enough to allow many juveniles to disperse after weaning before they were ever exposed to trapping. This latter possibility was only operative with regard to the "line trapping" where the traps were set once a month. Grid traps were set once a week so that juveniles would be exposed to traps within one week of weaning at the maximum. With regard to the first possibility, the body weights of the juveniles (40g or less when first captured) suggested that they were

recently weaned animals (see Section VI). The juveniles therefore it seems did not disperse before the first capture.

Thus it was concluded that the majority of the juveniles and sub-adults did not disperse, and that dispersal was by adults, both sexes dispersing in about equal numbers (Table 10).

In A. stuartii, also, the movements of the young animals were shorter than those of the older animals. Only three dispersion movements were recorded, all having been made by adults (Table 10). No juvenile dispersal was recorded, and there was good evidence that young A. stuartii, like the young of A. fuscipes, tended to remain near the natal home. During the 1964/65 breeding season the pouch young of three females were toe clipped just prior to their leaving the pouch. All six young from one female were caught for two months after weaning within the home range of the parent. During the winter four of them disappeared and were not recaught, and the other two (one male and one female) remained to breed in their natal area. Five out of eight of the second female's young were caught for two months after weaning within their natal area, two were still being caught there after five months and one, a female, bred on the area. Of the third female's young only three out of eight were ever caught, one disappearing after one month, one after six months, and one female remained and bred in the area. Since the latter two females had home ranges which only impinged onto the grid area the lower numbers of their young which were recovered was not surprising.

Thus it appeared that neither the young nor the adults of A. stuartii dispersed to any great extent. The extensive movements of the males during the breeding period (see Fig. 11) were therefore of great biological significance. Not only did they affect gene flow between neighbouring populations and, of particular importance due to the very short simultaneous

breeding season in A. stuartii, help to ensure that all or most of the females were found and impregnated, but also, where all the males and most of the females belonged to the same generation, and little dispersion took place, the extensive male movements at mating time would appear to be essential to prevent a considerable amount of inbreeding.

Though the data for M. cervinipes was not extensive, the pattern of movement appeared to be different from that of R. fuscipes and A. stuartii. The males tended to move slightly longer distances than the females during the breeding season, but the difference between the sexes was very much less than that in R. fuscipes and A. stuartii. This suggested that they might form stable pairs for breeding rather than the males being promiscuous as in R. fuscipes and A. stuartii. Unfortunately insufficient home range data was collected for M. cervinipes to show whether male and female home ranges formed coincident pairs or not.

Most work on rat movements has been carried out on Rattus norvegicus, a rat which shows a considerable degree of sociality. Movements and ranges tend to be small in this species (Davis 1953). Most recorded distances between successive captures were less than 40 ft. (12.2m), both in residential areas and on a farm. Home ranges were only 100 to 150 ft. (30.5 to 45.75m) in diameter, and dispersal movements were very limited with practically no movement between city blocks, and very little between farm buildings 100 ft. (30.5m) apart (Davis, Emlen and Stokes 1948). However Rattus species living away from human habitations have larger home range diameters which are more comparable with R. fuscipes - e.g. average home range diameter 200 ft. (61m) for R. rattus in Hawaii (Spencer and Davis 1950); 680 ft. (207.5m) for R. exulans and 1050 ft. (320.25m) for R. whiteheadi in Malayan rain forest (Harrison 1958). Harrison's figures are actually the diameters of circles within which

99% of the captures occurred.

A notable difference between R. fuscipes and the Malayan rats was that in the Malayan rats no difference in range size occurred between the sexes (Harrison 1958). However Miller (1958) recorded that much larger movements were undertaken by male individuals of Apodemus in the summer than in the winter, though the length of female movements varied very little, and were much smaller in the summer than the male movements. Miller also noted that the extended male movements were correlated with the breeding condition of the females, not of the males themselves. In both R. fuscipes and A. stuartii the greatly increased male movements occurred in the female breeding season. In R. fuscipes little seasonal difference in breeding condition of the males was detected. In A. stuartii the male and female animals come into breeding condition at the same time (Woolley 1966) and it was during this month (September) that male movements reached their maximum.

The movement patterns in A. stuartii during the breeding season were very similar to those recorded for the insectivore Sorex araneus by Shillito (1963b). During the breeding season females of this species hold home ranges and males wander widely. Shillito noted that it was not certain whether the extensive male movements were being carried out within a large home range or not. In the case of A. stuartii it has been suggested that they were within their home range. However in this study home range has been considered in a wider sense than defined by Shillito (1963b) for her work.

In other features of their movements S. araneus was quite different from A. stuartii. All juveniles dispersed from the nest and many continued dispersing for a period of two months or more in marked contrast to the evidence obtained for A. stuartii juveniles. Female S. araneus

often moved ranges during the breeding season, but females of A. stuartii did not appear to do so. Shillito also found she could divide the adults into "short range" and "long range" groups. It was not possible to divide adults of A. stuartii into such groups in this study partly perhaps because the grid area was too small. However a few adult males of A. stuartii did appear to move less widely than others. If trapping was carried out over a much larger area using a trap spacing of at least twice that used on the grid in this study a similar difference between individuals of A. stuartii might be found.

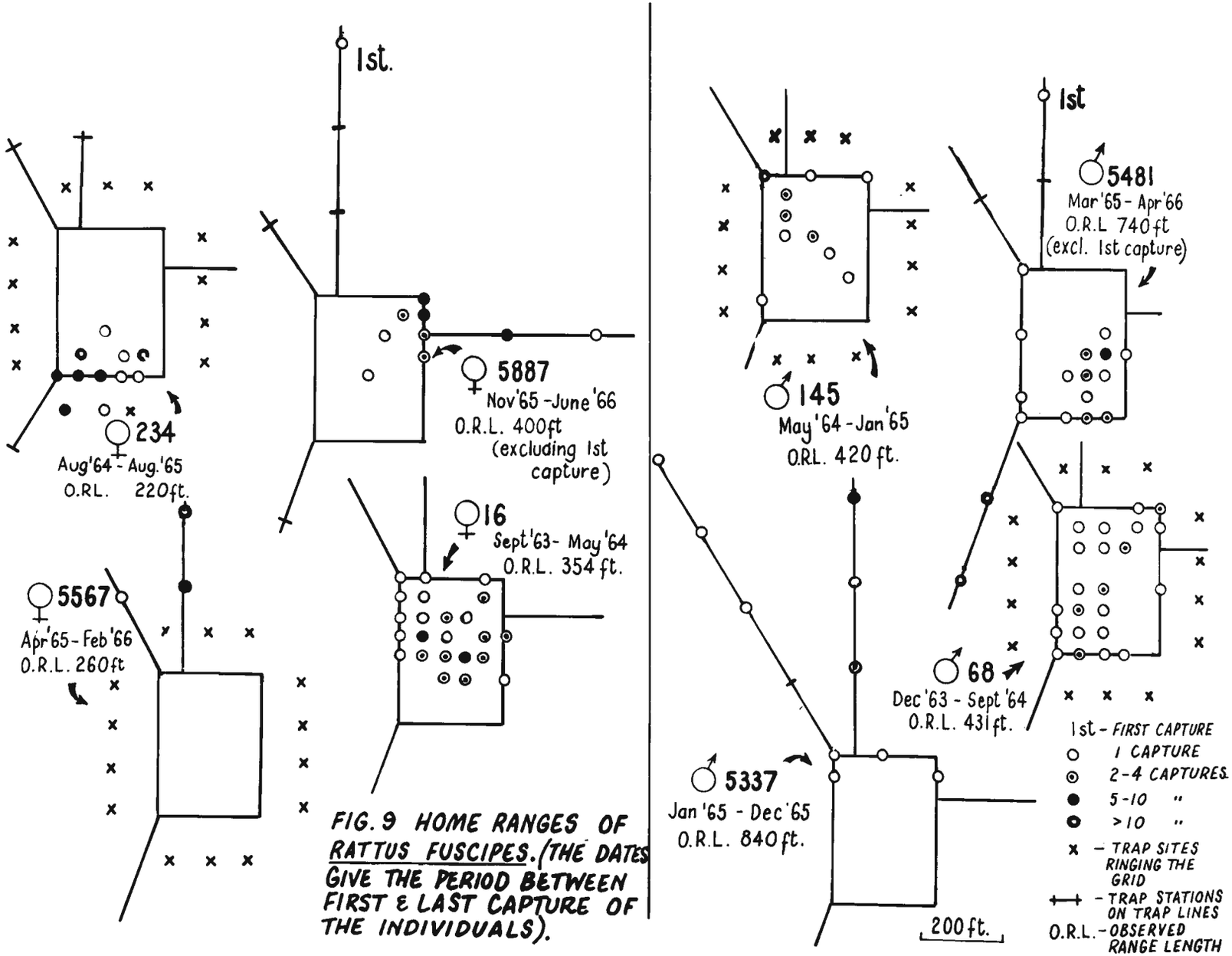


FIG. 9 HOME RANGES OF RATTUS FUSCIPES. (THE DATES GIVE THE PERIOD BETWEEN FIRST & LAST CAPTURE OF THE INDIVIDUALS).

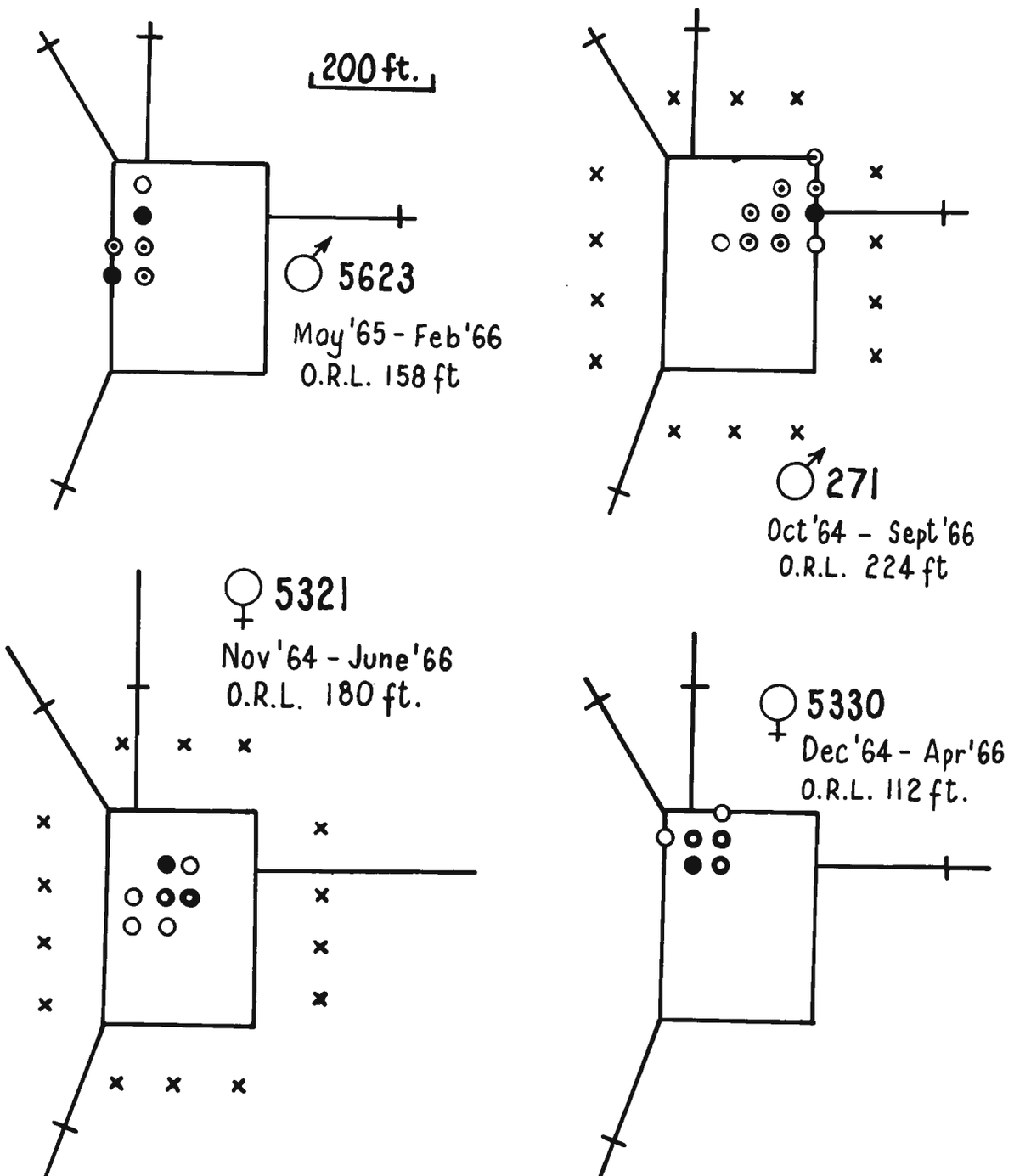


FIG. 10 HOME RANGES OF MELOMYS CERVINIPES (SYMBOLS AS IN FIG. 9).

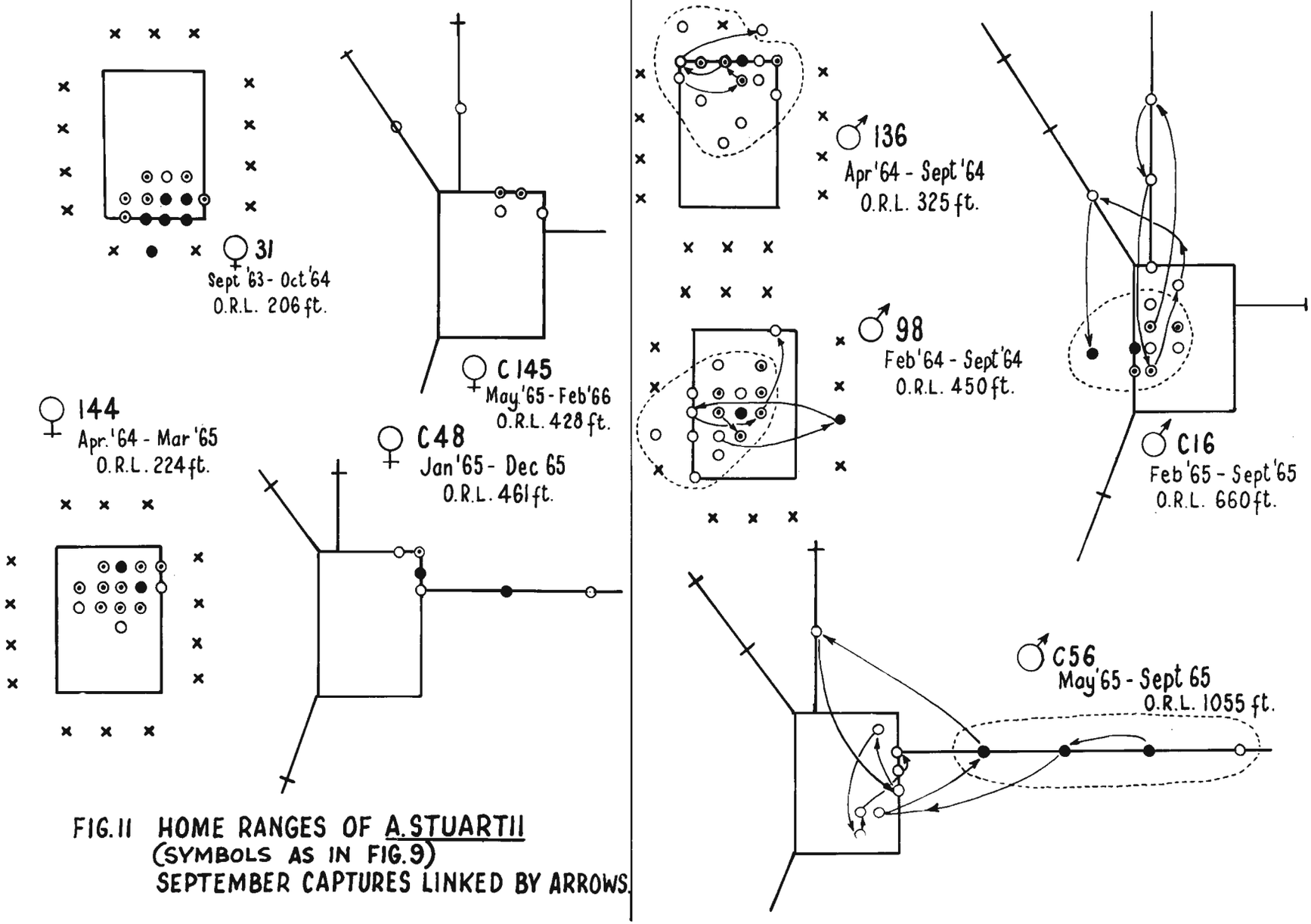


FIG. 11 HOME RANGES OF A. STUARTII
(SYMBOLS AS IN FIG. 9)
SEPTEMBER CAPTURES LINKED BY ARROWS.

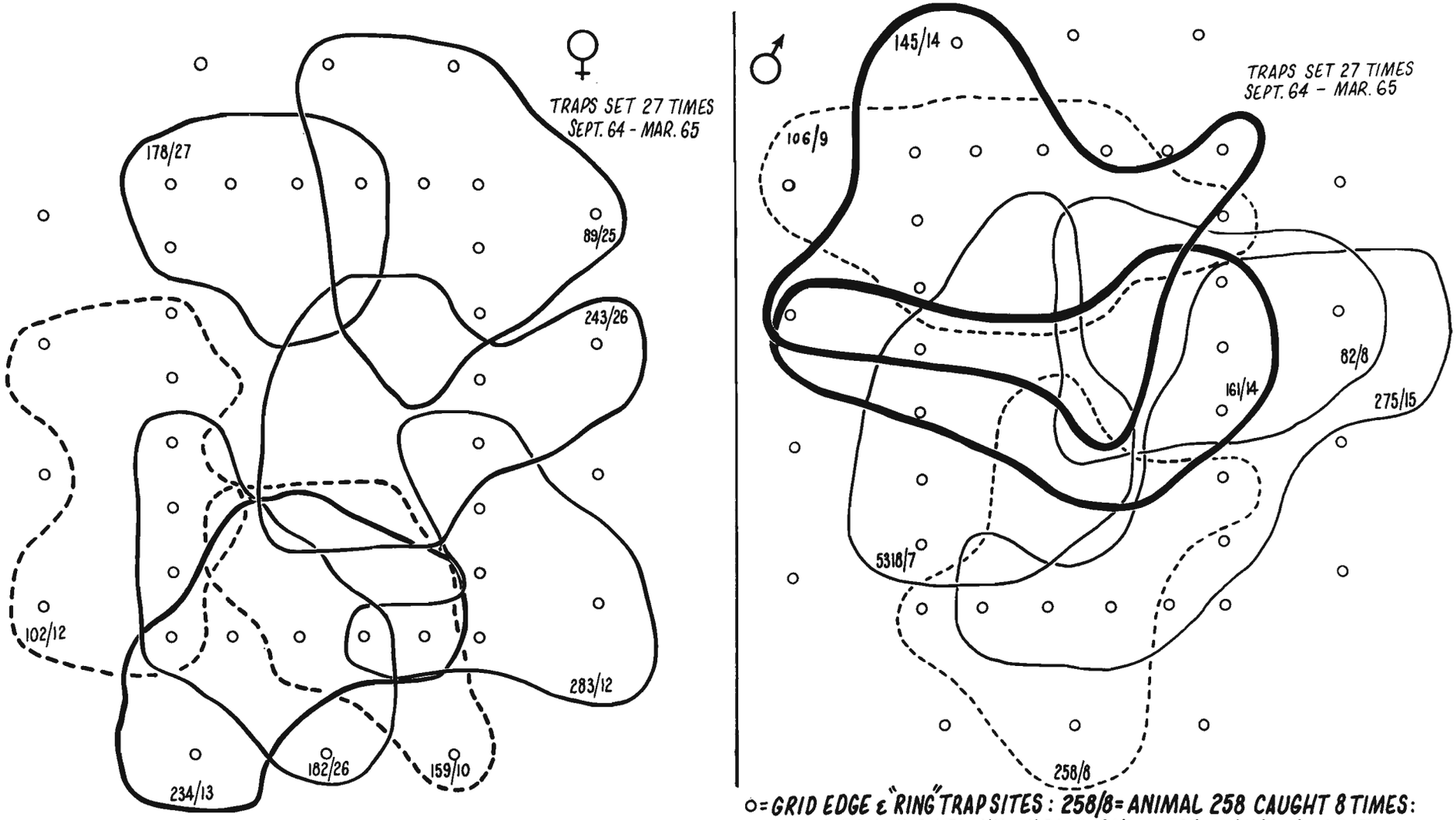
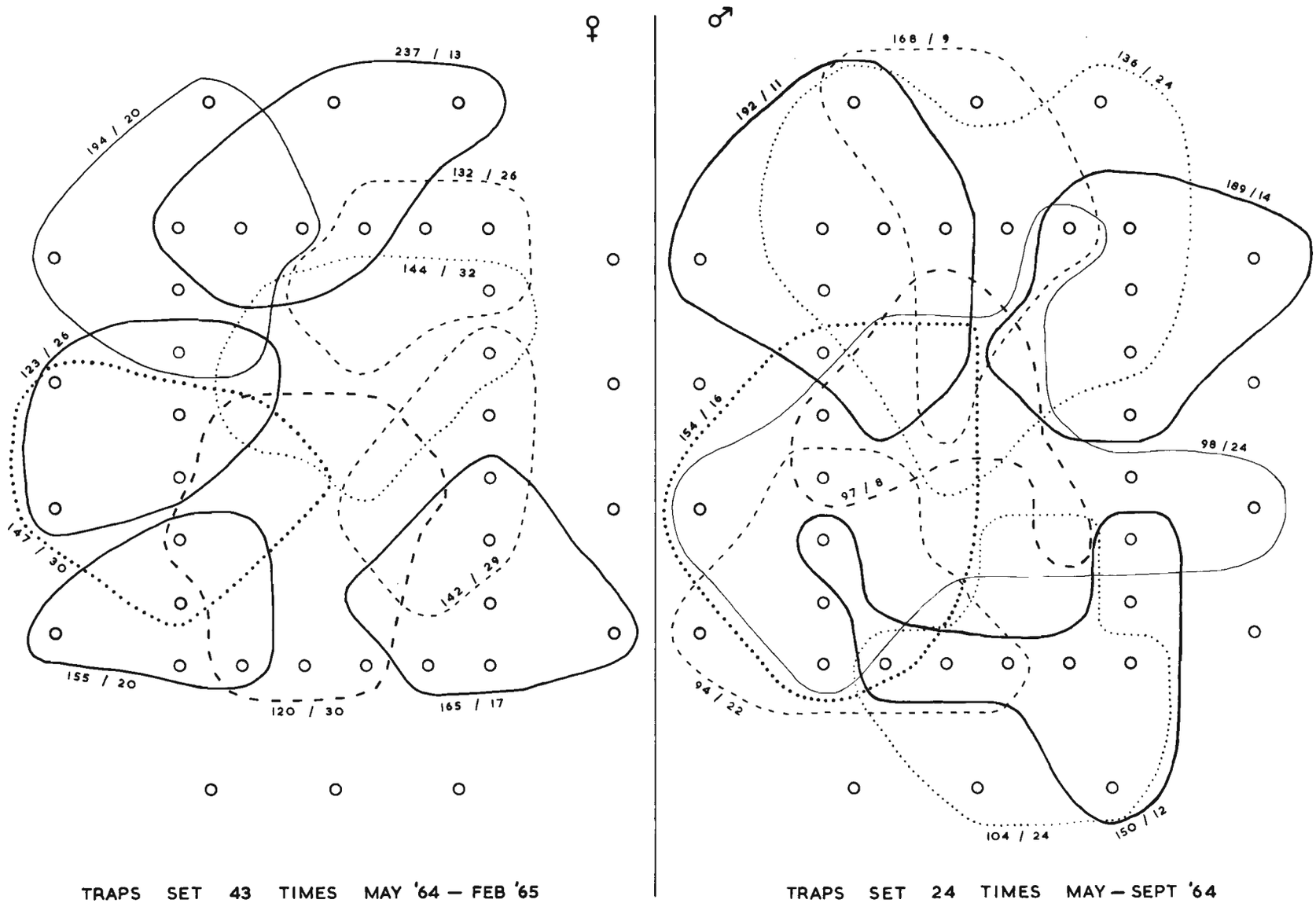


FIG. 12 RATTUS FUSCIPES TRAP REVEALED HOME RANGES 1964-65

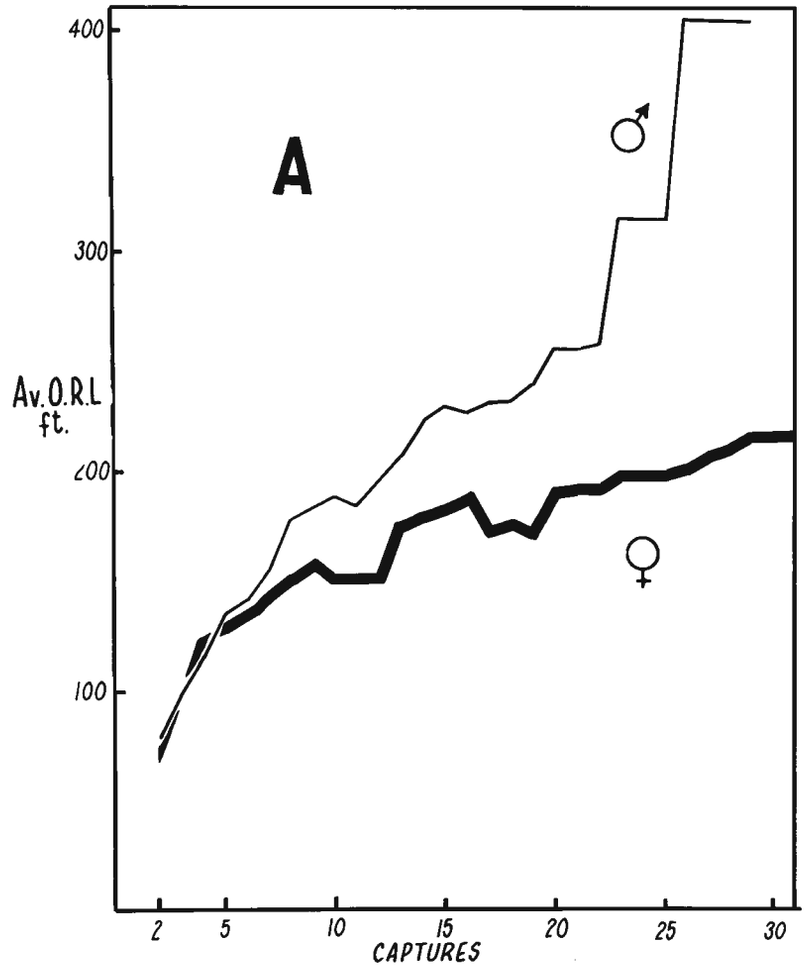
○ = GRID EDGE & "RING" TRAP SITES : 258/8 = ANIMAL 258 CAUGHT 8 TIMES: HOME RANGE OUTLINE VARIED ONLY FOR VISUAL CLARITY.

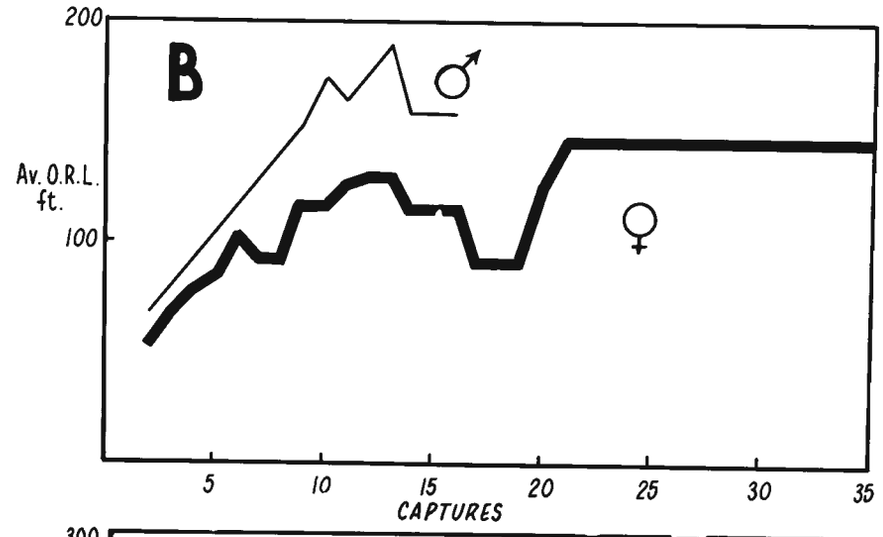


TRAPS SET 43 TIMES MAY '64 — FEB '65

TRAPS SET 24 TIMES MAY — SEPT '64

FIG 13 ANTECHINUS STUARTII TRAP-REVEALED HOME RANGES 1964/65
(FOR SYMBOLS SEE FIG. 12)





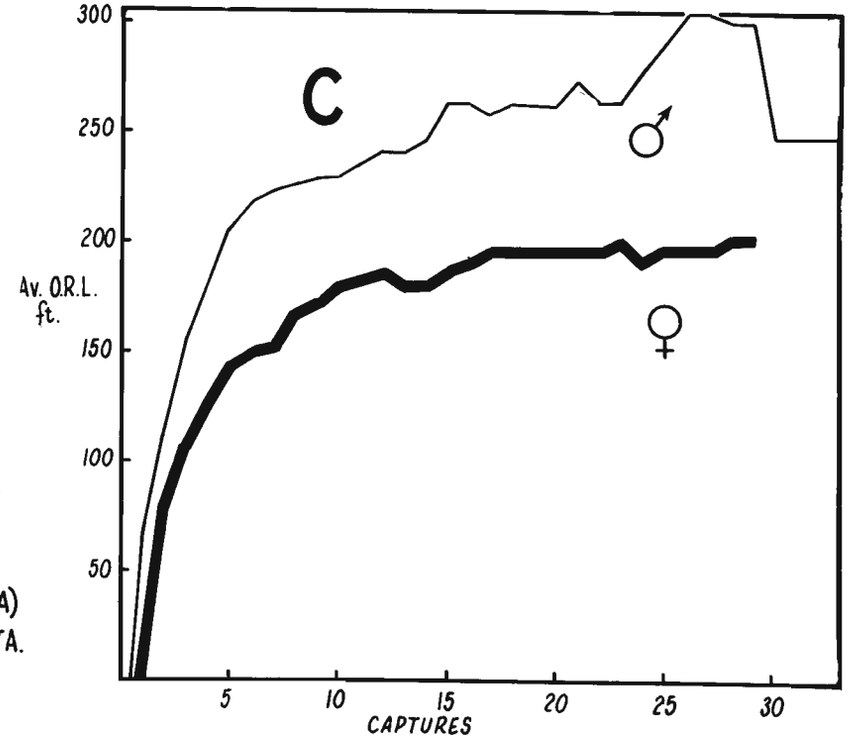
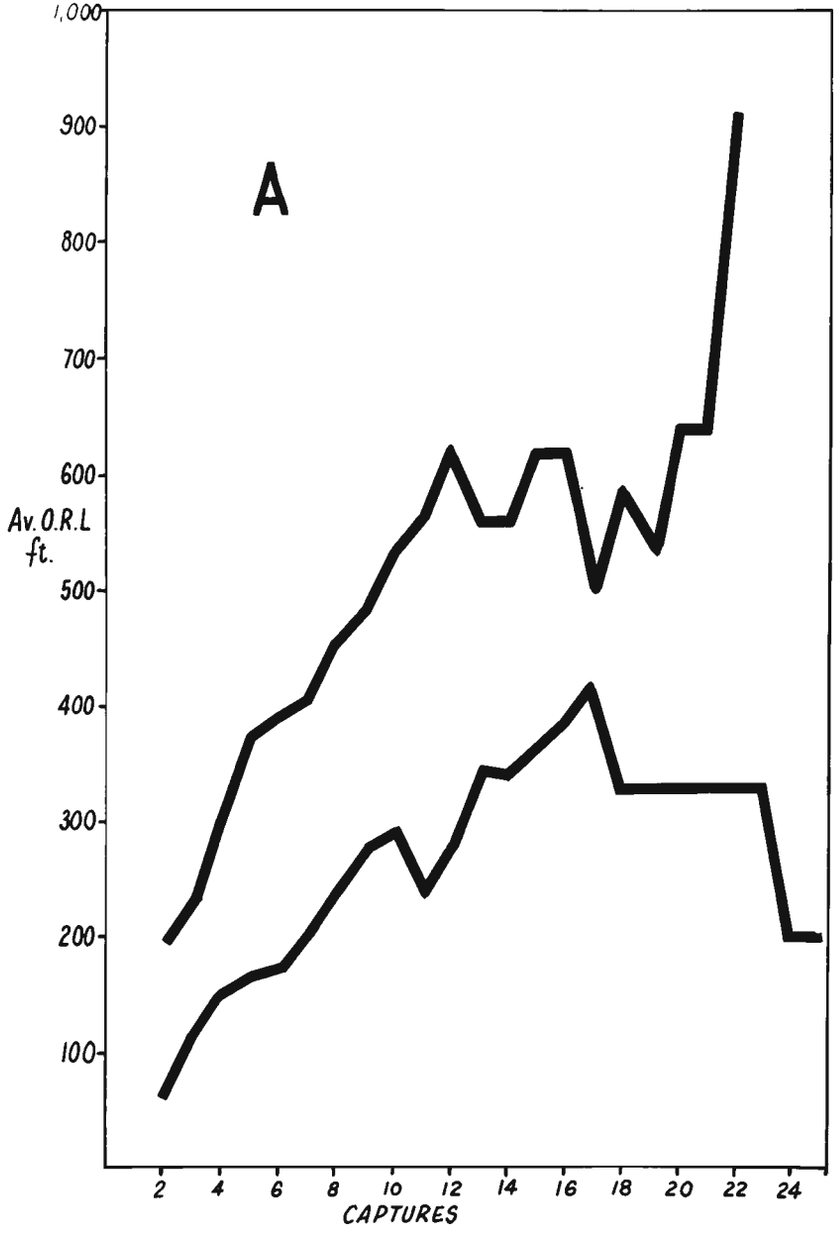


FIG.14 AVERAGE OBSERVED RANGE LENGTHS (Av. O.R.L.) AT CONSECUTIVE CAPTURES OF MALES & FEMALES OF A.STUARTII(A) M. CERVINIPES (B) & R.FUSCIPES(C) FROM "GRID TRAPPING" DATA.



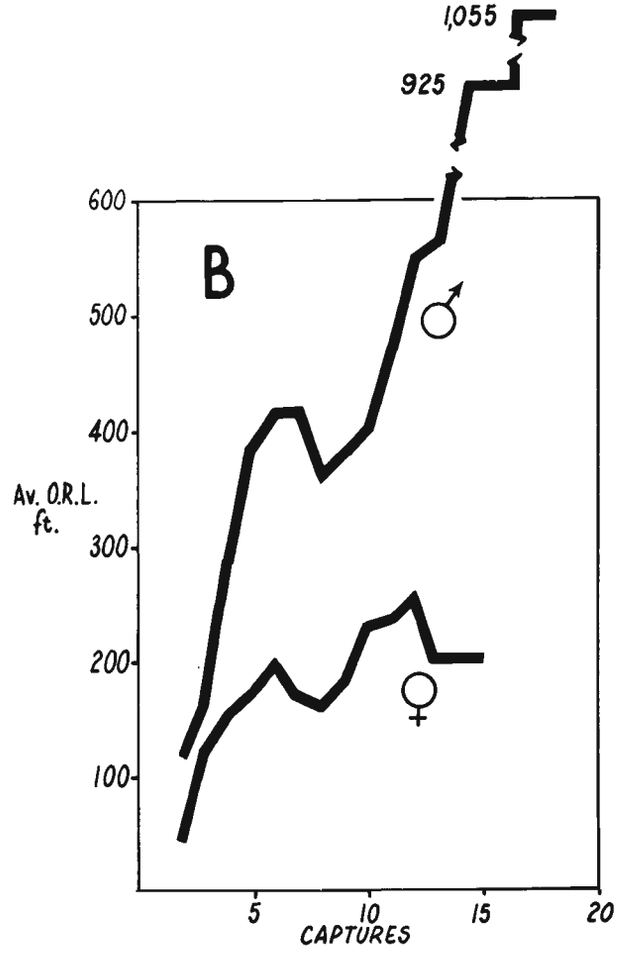


FIG. 15 AVERAGE OBSERVED RANGE LENGTHS (Av. O.R.L) AT CONSECUTIVE CAPTURES OF MALES & FEMALES OF R. FUSCIPES (A), A. STUARTII (B). FROM "LINE TRAPPING" DATA.

VIII MORTALITY

A. Methods

Monthly minimum survival rates were estimated by direct enumeration of the number known to be alive in one month and the number of these individuals known to have survived to the following month. In order to compare mortality rates between seasons, and between different sex and age groups, an average monthly survival rate was calculated. This was done by summing the numbers of animals known to be alive in all but the last month of the period (1, 2,....., t) in question ($\sum_{1}^{t-1} X_t$), then summing the numbers of individuals in all but the first month which were known to have survived from the previous month ($\sum_{2}^{t} Y_t$). Then $\sum_{2}^{t} Y_t / \sum_{1}^{t-1} X_t$ gave the average monthly survival factor.

Data from the period following April 1966 have not been used for the calculation of any average monthly survival rates. The time between trappings after this date was very much longer than that during the previous part of the study, and therefore any averages calculated from, or incorporating data from, this period would have been biassed in comparison with those calculated from the earlier data.

An index of early juvenile survival (the estimated number of young recruited to the population per litter) was obtained from the number of pregnancies or lactations recorded during a breeding season, and the total number of juvenile and sub-adult animals captured during the same year. In R. fuscipes dispersal movements which were found to be very

limited in the juvenile and sub-adult age groups would have had little effect on this index. However in A. stuartii the movement patterns seemed to have a marked effect on the number of new animals captured from May onwards. It was not possible to determine exactly to what degree movements were affecting the number of new animals captured (Section IX), therefore, on an arbitrary basis, unmarked animals caught up to and including May were used in estimating the index of early juvenile survival, but those caught in June and onwards were ignored.

Changes in average litter size between the different years, which were not investigated in R. fuscipes, would affect this index. However since there were no data on this subject, average litter size has been assumed to remain unchanged, and changes in the index have been discussed as changes in mortality of the nestlings. Litter size in A. stuartii showed no appreciable change during the study years.

B. Rattus fuscipes

(i) Results

The average monthly survival rates are presented in Table 11 and the monthly survival rates in Tables 12 and 13. The number of recaptures of most M. cervinipes individuals was low, and for this reason, and because of the relatively few individuals captured, mortality has not been analysed for this species.

The broad features of mortality in R. fuscipes (Table 11) were:

1. Adults and sub-adults generally survived better than the juveniles.
2. Adult females tended to survive better than males in all periods but the non breeding season of 1965.
3. Sub-adult females survived better than males in 1963/64. This was reversed in 1964/65.

Table 11 Average monthly survival rates and index of early juvenile mortality for R. fuscipes. Sample sizes in brackets.

	Juveniles		Sub-adults		Adults		Index of early juvenile mortality+
	♀	♂	♀	♂	♀	♂	
Yearly averages							
Nov. '63 - Oct. '64	0.67 (15)	0.73 (11)	0.83 (36)	0.76 (34)	0.81 (57)	0.66(116)	3.18 (11)*
Nov. '64 - Oct. '65	0.50 (14)	0.66 (32)	0.79 (43)	0.85 (74)	0.84(102)	0.77(133)	1.85 (27)*
Nov. '65 - Apr. '66**	0.55 (9)	0.40 (10)	0.00 (1)	1.00 (3)	0.80 (55)	0.67 (78)	1.80 (10)*
Seasonal averages							
Nov. '63 - Apr. '64 (breeding season)	0.67 (15)	0.73 (11)	1.00 (6)	0.89 (9)	0.79 (33)	0.70 (56)	-
May '64 - Oct. '64 (nonbreeding season)	-	-	0.80 (30)	0.72 (25)	0.83 (24)	0.62 (60)	-
Nov. '64 - June '65 (breeding season)	0.50 (14)	0.66 (32)	0.83 (29)	0.89 (47)	0.90 (81)	0.72 (79)	-
July '65 - Oct. '65 (nonbreeding season)	-	-	0.71 (14)	0.78 (27)	0.73 (41)	0.85 (54)	-

\+ estimated number of young recruited to the population per litter.

* estimated number of litters from pregnant and lactating animals captured.

** regular "grid trapping" ceased at the end of April 1966.

4. Sub-adults survived slightly better in the breeding season than the non breeding season.

5. The juvenile males survived slightly better than the females in the 1964/65 season.

The more detailed analysis of mortality given by the monthly minimum survival rates (Tables 12 and 13) showed the following features:

1. The adult female survival rates tended to be lower at the end of or just after the breeding season (i.e. April and May 1964, July and August 1965).

2. In general the adult male survival rates were lower immediately prior to or early in the breeding season (i.e. September to January). They were very low in December 1965 and January 1966.

3. With the exception of the above mentioned instances and the unreliable results from the small samples, adult monthly survival rates were relatively constant for each sex throughout the study.

4. Sub-adult survival rates were relatively constant in both the females and the males, and the variations which occurred can in most cases be attributed to small sample size.

5. In February and March 1965 juvenile male survival rates were much higher than on the average though juvenile female survival rates were low, at least in February.

6. In January 1966 the survival rates of both female and male juveniles were low.

7. The early juvenile survival rate was considerably higher in the 1963/64 season than in the 1964/65 and 1965/66 seasons (Table 11), though the latter season is not strictly comparable since regular grid trapping stopped in April 1966.

Table 12 Minimum survival rates/month of female R. fuscipes. Sample sizes in brackets.

	Juveniles	Sub-adults	Adults
1963			
September		1.00 (2)	0.75 (8)
October			0.70 (10)
November			0.86 (7)
December			0.71 (7)
1964			
January			1.00 (5)
February	0.66 (3)	1.00 (1)	0.80 (5)
March	1.00 (1)	1.00 (3)	0.75 (4)
April	0.33 (3)	1.00 (2)	0.60 (5)
May	1.00 (3)	0.80 (5)	0.33 (3)
June	0.66 (3)	0.70 (10)	0.00 (1)
July	0.50 (2)	1.00 (7)	
August		0.75 (4)	1.00 (5)
September		1.00 (2)	0.88 (8)
October		0.50 (2)	1.00 (7)
November			0.89 (9)
December		1.00 (1)	0.78 (9)
1965			
January		1.00 (1)	0.91 (11)
February	0.17 (6)	1.00 (3)	0.78 (9)
March	1.00 (3)	0.80 (5)	0.89 (9)
April	0.50 (2)	0.60 (5)	0.92 (12)
May	1.00 (1)	1.00 (7)	1.00 (11)
June	1.00 (1)	0.71 (7)	1.00 (11)
July	0.00 (1)	0.60 (5)	0.62 (13)
August		0.83 (6)	0.67 (9)
September		0.50 (2)	0.90 (10)
October		1.00 (1)	0.78 (9)
November			0.67 (12)
December			0.69 (13)
1966			
January	0.33 (3)		0.75 (12)
February	0.67 (3)		1.00 (9)
March	1.00 (2)	0.00 (1)	1.00 (9)
June	$\frac{0.00}{(0.00)+(1)}$	$\frac{0.63}{(0.33)+(3)}$	$\frac{1.00}{(1.00)+(9)}$
September		$\frac{0.00}{(0.00)+(2)}$	$\frac{0.80}{(0.50)+(10)}$
December			$\frac{0.72}{(0.43)+(7)}$

+ Proportion of those caught in previous trapping known to be alive (P_t). Minimum survival rate per month underlined = 1 - death rate; obtained by using $- \log_e P_t / W\ t$ = death rate (Leslie et al 1953 ($W\ t$ = 1 when interval between trappings - 1 month)

Table 13 Minimum survival rates/month of male R. fuscipes
Sample sizes in brackets.

	Juveniles	Sub-adults	Adults
1963			
September		1.00 (1)	0.50 (6)
October			0.60 (5)
November			0.73(11)
December			0.38(13)
1964			
January			0.89 (9)
February	1.00 (3)	1.00 (1)	0.71 (7)
March	0.75 (4)	1.00 (2)	0.88 (8)
April	0.33 (3)	0.83 (6)	0.75 (8)
May	- (0)	0.86 (6)	0.50(12)
June	1.00 (1)	0.63 (8)	0.86 (7)
July		0.66 (6)	0.75 (8)
August		1.00 (3)	0.66 (9)
September		0.00 (1)	0.64(11)
October			0.69(13)
November	1.00 (1)		0.50(12)
December	0.00 (1)	1.00 (1)	0.67 (9)
1965			
January	0.50 (6)	1.00 (1)	0.78 (9)
February	0.89 (9)	0.50 (2)	0.73(11)
March	0.75 (8)	0.75 (8)	0.70(10)
April	0.50 (2)	0.82(11)	0.80(10)
May	0.67 (3)	1.00(11)	0.80(10)
June	0.00 (1)	1.00(13)	0.88 (8)
July	0.00 (1)	0.77(13)	0.78 (9)
August		0.86 (7)	1.00(11)
September		0.66 (6)	1.00(14)
October		1.00 (1)	0.70(20)
November			0.82(22)
December			0.58(24)
1966			
January	0.17 (6)		0.50(16)
February	0.67 (3)		1.00 (7)
March	1.00 (1)	1.00 (1)	0.66 (9)
June	$\frac{0.00}{(0.00)+(1)}$	$\frac{1.00}{(1.00)+(1)}$	$\frac{0.94}{(0.83)+(6)}$
September			$\frac{0.86}{(0.66)+(6)}$
December			$\frac{0.80}{(0.50)+(8)}$

\+ see Table 12.

(ii) Discussion

Since mortality was equated to disappearance from the trapping area emigration losseswere also included in the results. These losses might have been due to residents dispersing or to transients. In R. fuscipes dispersal movements did occur (section VII) and during certain periods of the year transients were relatively numerous (section VII). In both cases it was mainly adult animals which were involved and as a result some of the estimated adult survival rates may be slightly biassed.

The generally better survival of the adult females compared with the adult males was not in agreement with survival rates for Malayan rats given by Harrison (1956). Out of the eleven species studied by him, in only one, Rattus rattus diardii, did the females survive better than the males. In the remainder survival rates were about the same for both sexes. However it has been shown for Clethrionomys glareolus in England (Newson, 1963) and for Microtus californicus in California (Krebs, 1966) that the females in these species generally survived better than the males. Both the latter workers found survival rates varied considerably between the sexes, age groups and seasons. Excluding variations due to small sample sizes, and a few seasonal variations of short duration, the survival rates of adult and sub-adult R. fuscipes were comparatively constant. In the early juvenile and juvenile age groups though,more marked variations occurred.

The changes in the survival rates of the juvenile animals (weanlings) seemed to be related to changes in the population size, in contrast to the findings for Microtus californicus by Krebs (1966, p.270); "Weanling and early juvenile mortality was not clearly related to the population changes". Thus the large population of R. fuscipes in 1965 appeared to be

related to the high survival rates of the juvenile males in February and March of that year (Fig. 21). Also the low numbers of animals in the 1966 population appeared to be related to the low survival rates of both male and female juveniles during the 1965/66 breeding season (Figs. 20 and 21), though other factors were also involved in this case (see Section IX). However the early juvenile survival rates at Mt. Glorious were not related to the population changes in a constant manner. Thus though they were low in 1965/66 when the total population did not increase during the breeding season, they were also as low in the previous breeding season when the population showed a marked rise.

The more or less constant survival rates for the sub-adult and adult animals were comparable to those found in Malayan rats by Harrison (1956), though in the Malayan species the constant survival rate applied to animals of all ages after weaning. It seemed doubtful whether this would have been so for R. fuscipes even had larger juvenile samples been obtained so that a more reliable estimate of juvenile survival rates could have been made.

Table 14 Average monthly survival factors and index of early juvenile mortality for A. stuartii. Sample sizes in brackets.

	1964	1965	1966
Feb. - Aug.			
Males	0.79 (117)	0.69 (87)	-
Non parous females	0.93 (76)	0.79 (62)	-
Parous females	0.88 (26)	0.86 (63)	-
	1963/64	1964/65	1965/66
Sept - Feb.			
Parous females	0.69 (33)	0.90 (73)	0.90 (24)
Index of early juvenile survival+	3.90 (10)*	2.75 (16)*	3.10 (10)*

\+ see Table 11.

* Known number of litters carried to end of pouch life of the young.

C. Antechinus stuartii

(i) Results

The average monthly survival rates for non parous females and males in Table 14 were based on the data for the months of February to August since males suffered 100% mortality in September. Comparison between the sexes is therefore necessarily limited to the February - August period. The main points shown by these data were:

1. Females tended to survive better than males.
2. In 1964 both non parous females and males survived better than in 1965.
3. Early juveniles survived better in the 1963/64 breeding season than in the 1964/65 breeding season.

The monthly survival rates (Tables 15 and 16) were calculated separately for each year class (i.e. animals born in the same year). These showed that:

1. The survival rates of the parous females over the period of September 1963 to February 1964 were much lower than during the same period in the 1964/65 and 1965/66 seasons.
2. The survival rates of the parous females were generally lowest in February or March (i.e. just after weaning) each year.
3. Low survival rates were recorded for both males and non parous females of the 1964/65 year class in February, July and August in 1965.
4. All male animals died during the latter part of September or early October each year.

Table 15 Minimum survival rates/month of female A. stuartii. Sample sizes in brackets. (Records below the dashed line in each year class are for parous females, those above for non parous females).

	1962/63 year class	1963/64 year class	1964/65 year class	1965/66 year class
1963				
September	0.45 (11)			
October	0.86 (7)			
November	0.66 (6)			
December	0.80 (5)			
1964				
January	1.00 (4)			
February	0.66 (6)	1.00 (2)		
March	1.00 (4)	1.00 (6)		
April	1.00 (4)	1.00 (11)		
May	1.00 (4)	1.00 (11)		
June	1.00 (4)	0.75 (16)		
July	1.00 (4)	1.00 (15)		
August	0.75 (4)	0.87 (15)		
September	0.66 (3)	1.00 (14)		
October	0.50 (2)	0.94 (16)		
November	0.50 (1)	0.87 (16)		
December	1.00 (1)	0.92 (13)		
1965				
January	1.00 (1)	0.93 (14)	1.00 (3)	
February	1.00 (1)	0.86 (14)	0.44 (9)	
March	0.00 (1)	0.69 (13)	1.00 (5)	
April		1.00 (9)	1.00 (9)	
May		1.00 (9)	0.91 (11)	
June		0.66 (9)	0.91 (11)	
July		0.57 (7)	0.70 (10)	
August		1.00 (4)	0.57 (7)	
September		1.00 (4)	1.00 (4)	
October		1.00 (4)	1.00 (5)	
November		1.00 (4)	0.83 (6)	
December		1.00 (4)	0.80 (5)	
1966				
January		1.00 (4)	1.00 (4)	
February		0.25 (4)	0.75 (4)	1.00 (1)
March		1.00 (1)	0.67 (3)	1.00 (8)
June		1.00 / (1.00)+(1)	1.00 / (1.00)+(2)	0.82 / (0.70)+(10)
September		0.00 / (0.00)+(1)	0.63 / (0.33)+(3)	0.73 / (0.45)+(11)
December			0.00 / (0.00)+(1)	0.94 / (0.83)+(6)

+ See Table 12.

Table 16 Minimum survival rates/month of male A. stuartii. Sample sizes in brackets.

	1963/64 year class	1964/65 year class	1965/66 year class
January	1.00 (1)		
February	0.90 (10)	0.58 (12)	0.00 (1)
March	0.77 (13)	0.75 (16)	1.00 (8)
April	1.00 (14)	1.00 (14)	
May	0.76 (17)	0.60 (15)	
June	0.74 (26)	0.85 (13)	0.90 (0.82)+(11)
July	0.84 (19)	0.36 (11)	
August	0.76 (17)	0.50 (6)	0.62 (0.32)+(19)
September	0.00 (29)	0.00 (8)	0.00 (12)

\+ see Table 12

(ii) Discussion

Dispersal movements in A. stuartii were rare (Section VII), and the number of transients on the grid relatively low, except in the case of males in September, in which month mortality was 100% and would not be affected by movements. Thus in this species movements probably had little effect on estimated survival rates.

The differences in the survival rates between sex and age groups, which are presented above, had marked effects on the size and structure of the population between years. These are discussed in Section IX.

The survival of early juveniles in this species was constantly related to changes in the size of the population. In the 1963/64 season the early juvenile survival rate was high and in the winter the population attained its largest size for the three study years. The early juvenile survival rate was lowest in the 1964/65 season and in 1965 the population size in the winter was the lowest recorded in the three years. In the 1965/66 season the early juvenile survival rate was again high, and though

the population size in the winter of 1966 was not much greater than in 1965, the increase in size from the beginning of the breeding season up to early winter was much greater than in 1965 (Fig. 19).

That all the adult males died at the end of September there was little doubt, even though with intensive searching no bodies were found in the field. However, this was perhaps not surprising in view of the nature of the forest floor which was for the most part a jumble of basalt blocks with a large number of nooks and crannies.

The latest time in the year that adult males were caught was October 3rd in 1965 when three males were caught in the "line trapping" of that night. One of these three was dead in the trap and the other two were in moribund state and did not recover. All the females caught on that night were in a healthy active condition at the time of clearing the traps. Further supporting evidence that the males died was that no males have ever been recaptured in their second year of life.

The possibility that the males might have moved to another area or habitat type was examined in 1964. Immediately following the first night (October 2nd) that no males were caught on the grid during the regular trapping, a week's trapping (40 traps per night) was carried out in grassland, lantana, eucalypt forest and other rain forest patches in the same general locality as the study area. No male individuals of A. stuartii were caught, though 15 females were trapped mainly in the lantana and the other rainforest areas. It was therefore concluded that in the field all the males died at the end of September.

IX POPULATION STRUCTURE AND SIZE FLUCTUATIONS

A. Methods

Monthly estimates of the population of each of the species were made using a modified Lincoln Index (Bailey, 1951):

$$N^1 = C_0.(C_1 + 1)/(S_1 + 1)$$

$$V(N^1) = (N^1)^2.(C_1 - S_1)/(C_1 + 1).(S_1 + 2)$$

where C_0 was the total number of animals caught in the first half of the month; C_1 was the total number of animals caught in the second half of the month; and S_1 was the number of recaptures (Appendices 4 - 9). Marked animals which were caught in the second half of any month but not in the first half of the same month were treated as new captures for the estimation of that month's population size. In June, September and December 1966 when the only trapping carried out was that of the "activity trapping" sequence, the records from the first and last trapping nights in each month were used for the population estimates. "Tree trapping", "ring trapping" and "line trapping" were ignored in all estimates of the population size.

Monthly figures for the population size for each species were also obtained from the number of animals known to be alive in each month from their previous and subsequent capture records (Appendices 5, 7 and 9).

For R. fuscipes and A. stuartii the results from the two methods were comparatively similar (Figs. 16 and 19). Many of the differences, particularly in the case of A. stuartii, were underestimates by the Lincoln Index when compared with the numbers which were known to be alive. At least two of the assumptions in the theory of the Lincoln Index method of estimation, namely

absence of dilution, and equal probability of capture for all animals, were not valid for the Mt. Glorious populations. Breeding and the presence of transient animals (see below) caused dilution, and many animals were trap prone, being caught at nearly every trapping. Because of these factors the "known to be alive" figures have been used in all discussions on population size, not the Lincoln Index estimates.

The validity of comparing differences in population size based on "known to be alive" figures depends on whether the trapping effort, and the percentage of the population which was trappable, varied significantly between comparative periods or not. Trapping effort was constant at 192 trap nights per month, except for the first few months of the study when 288 trap nights per month were operated (N.B. the change from 288 to 192 trap nights per month was made because the extra 96 trap nights were giving no extra useful information). Now it appeared that the "overall trappability" of the trappable animals did not vary significantly between years, since, if it had, it would have been expected that the relationship between the "known to be alive" curve and the Lincoln Index curve would have varied greatly between years (the curves approaching closer to each other if "trappability" increased, or diverging from each other if "trappability" decreased), and it did not. Thus it seemed a reasonable assumption that the percentage of the population which was trappable did not vary between years either.

Owing to the poor trappability of individuals of M. cervinipes the population estimates were less reliable than those of the other two species. However, where population figures have been discussed they also refer to the numbers known to be alive, since in most months these figures exceeded the Lincoln Index estimates (Fig. 17). All population figures refer to the number of animals present on the grid at any particular time, and do not necessarily represent the density of animals per unit area.

Theoretically the individuals forming a small mammal population can be divided into residents -- animals which occupy a home range within which they usually have one or more relatively permanent homesites, and transients -- animals wandering haphazardly without a permanent homesite. In a live trapping study the assignment of individuals to either of these two categories is subjective. The criteria usually used are the number of captures of an individual, and the length of the time interval between the first and last capture. It is assumed that an animal without a home range, wandering through an area being trapped (i.e. a transient), will be captured only a few times during a period of short duration, and then will never be seen again; and that an animal occupying a home range, partly or wholly within the trapping area (i.e. a resident), will be captured often, and for a prolonged period of time. Animals caught only a few times, but with long intervals between captures, are usually assumed to be "trap shy" residents.

At.Mt. Glorious animals caught three times or more have been designated residents, and those caught only once or twice, transients. The division was drawn between two and three captures, because the frequency distributions of the number of captures, showed a marked change in slope between two and three captures in both the male and female R. fuscipes (Fig. 26), and to

a lesser degree in the males and females of A. stuartii (Fig. 27), this criteria having been used by Blair (1951) to distinguish between residents and transients. However the use of the number of captures alone is not entirely satisfactory. Thus animals at Mt. Glorious with only three captures, all of which were in one month, were only considered residents if at least one capture occurred in both the first and second halves of the month. The period of residence could then be assumed to be one month. The additional criterion usually used to designate transients -- a short time interval between first and last capture, was not used, because the line trapping, which afforded data on the movements of animals outside the grid area, showed that individuals, with only two grid captures widely spaced in time, were very infrequent visitors (not more than one visit in four months) to the grid area, not "trap shy" residents.

Thus, during the line trapping (March 1965 -- February 1966), 16 female and 18 male R. fuscipes individuals were caught only once or twice on the grid. Seven of these females (44%) and eleven of the males (61%) were known from the line trapping to be residents in areas at least 200 feet (61m) from the grid, suggesting that their one or two grid captures occurred during "exploratory sallies". Similarly three out of four females (75%) and six out of eight males (75%) of A. stuartii, caught only once or twice on the grid, were known to be residents well outside the grid area. Considering the locations of the lines relative to the grid (Fig. 1), a population of unmarked animals must have been present in those areas of the forest around the grid,which were not sampled by the lines. It seems reasonable to assume that a proportion of these animals were also "once or twice caught" visitors to the grid during the same period. Thus certainly more than 50%,

and probably 75% of the animals caught once or twice only on the grid were infrequent visitors. All those animals with two grid captures widely spaced in time were known to be in the "infrequent visitors" class. Though each of these animals had a home range, and was not just a "wanderer", they have been included in the transient group, since it appeared that the relationship between these animals and the "grid residents", at least on a temporal basis, was similar to that between "true" transients and "grid residents". All other animals with only one or two captures on the grid were assumed to be normal transients.

Since juveniles of R. fuscipes entered the trappable population at about one month old, and grew to sub-adults by the end of the following month, they would only be exposed to trapping on about four occasions. It seemed probable therefore that many might not be caught more than once or twice even though they were resident on the grid area. Therefore they have been ignored in the analysis of resident and transient animals. Further, no analysis of resident and transient individuals was carried out for the populations present during the first and last three months of the "grid trapping" sequence in any of the species, nor for June, September and December 1966, since it was not possible under the terms of the definition to determine whether the unmarked animals caught in these months were transients or not. Nor was it possible to divide the M. cervinipes population into transient and resident individuals owing to their very poor trappability.

In order to investigate recruitment, the populations of the three species were divided into year classes of animals born in the same breeding season on the basis of age at first capture. Age was estimated

from body weight in R. fuscipes and M. cervinipes. In A. stuartii exact age was known from birth dates.

B. Rattus fuscipes

(i) Results

Each year the numbers of R. fuscipes rose during the summer or early autumn, and then fell away to a winter/spring plateau from which numbers rose again the following summer (Fig. 19). However the fluctuations were not large, and in none of the years during the study did the population more than double from the pre-breeding season (winter/spring) level.

The first young (about one month old) began to enter the trappable population in Janaury and February (mid to late summer) each year (Figs. 20 and 21). At this time the previous seasons year class consisted entirely of adults. Sometime during the autumn and winter adult numbers usually fell, and few adults survived to a second main breeding season.

The population reached its highest level during the 1964/65 breeding season, and numbers remained higher than usual during the following winter. In 1966 the annual recruitment of young was very low, and the population level dropped to about the same level as at the beginning of the study in September 1963 (Figs. 20 and 21).

There were a considerable number of transient animals recorded in the population (Fig. 22). During the period from October 1963 to January 1966, 24 transient females and 48 transient males were captured: 19 of the females and 41 of the males were adult animals and five females and seven males were sub-adults. The high proportion of adults amongst the transient animals was statistically significant - X^2 = 8.16, 1 d.f., $0.001 < P < 0.01$ for females; X^2 = 24.08, 1 d.f., $P < 0.001$ for males. The percentage of transients each month was variable. In the female section

Table 17 The monthly sex ratios for the R. fuscipes population and the results of X^2 tests (significant results underlined), and using Yates' correction for continuity where the unadjusted X^2 was larger than the tabulated X^2 for P = 0.05

Month		Males	Females	X^2	P
1963	Sept.	6	10	1.00	> 0.30
	Oct.	7	10	0.52	> 0.30
	Nov.	11	7	0.88	> 0.30
	Dec.	13	6	2.56	> 0.10
1964	Jan.	--	--	----	----
	Feb.	11	8	0.48	> 0.30
	Mar.	15	9	1.50	> 0.20
	Apr.	--	--	----	----
	May	16	13	0.30	> 0.50
	June	15	14	0.02	> 0.80
	July	13	9	0.72	> 0.30
	Aug.	12	9	0.42	> 0.50
	Sept.	13	9	0.72	> 0.30
	Oct.	13	8	1.18	> 0.20
	Nov.	12	8	0.80	> 0.30
	Dec.	11	10	0.04	> 0.80
1965	Jan.	16	12	0.56	> 0.30
	Feb.	23	18	0.60	> 0.30
	Mar.	25	16	1.96	> 0.10
	Apr.	23	17	0.30	> 0.50
	May	22	18	0.40	> 0.50
	June	18	17	0.02	> 0.80
	July	18	17	0.02	> 0.80
	Aug.	14	13	0.03	> 0.80
	Sept.	16	12	0.56	> 0.30
	Oct.	17	10	1.80	> 0.10
	Nov.	18	13	0.80	> 0.30
	Dec.	18	14	0.50	> 0.30
1966	Jan.	18	15	0.26	> 0.50
	Feb.	8	11	0.46	> 0.50
	Mar.	8	13	1.18	> 0.20
	Apr.	5	14	3.36	> 0.05
	June	4	14	4.26	< <u>0.05</u>
	Sept.	7	9	0.24	> 0.50
	Dec.	11	6	1.46	> 0.30

Table 18 The sex distribution for the different age groups of the total number of R. fuscipes at first capture on the grid, and the results of X^2 tests.

	Males	Females	X^2		P
Adults	91	54	9.44	<	0.01
Sub-adults	22	14	1.76	>	0.10
Juveniles	44	27	4.06	<	0.05
Juveniles excluding the 1964/65 breeding season	17	15	0.125	>	0.70

Table 19 The number and sex of the young in litters of R. fuscipes, M. cervinipes, and A. stuartii.

Month of birth	Number in litter	Number of Males	Number of Females
R. fuscipes			
Oct. 1966	4	1	3
Dec. 1966	3	0	3
Jan. 1967	5	3	2
Feb. 1967	5	2	3
	6	4	2
	6	4	2
	4	2	2
March 1967	5	3	2
	4	2	2
	5	3	2
	5	2	3
April 1967	2	1	1
	3	1	2
Total	57	28	29
Average number/litter	4.4	2.2	2.2
M. cervinipes			
Nov. 1966	2	1	1
Dec. 1966	2	1	1
	2	1	1
Jan. 1967	1	0	1
Feb. 1967	2	2	0
	2	1	1
Total	11	6	5
Average number/litter	1.8	0.9	0.9
A. stuartii			
Oct. 1964	7	4	3
Nov. 1964	8	4	4
	8	4	4
	6	3	3
Nov. 1965	7	3	4
	8	4	4
Total	44	22	22
Average number/litter	7.3	3.6	3.6

of the population there was a tendency for more transients to occur at the end of the breeding season. The number of female transients in 1964 was lower than in 1965 (Fig. 22). In the male section of the population there was a general increase in the percentage of transients prior to and early in the breeding season, and a fall off in their numbers from the middle of the breeding season onwards. During the winter the percentage of male transients in the population was comparatively low (Fig. 22).

Though the number of females in the population in any one month was nearly always less than the number of males the differences were not statistically significant, except during June 1966 when there were more females in the population than males (Table 17). The sex ratio within age (at first capture) groups for all animals captured on the grid (Table 18) showed more males than females were caught in all three age categories. However the differences were statistically significant only in the adult and juvenile age groups. The sex ratio of the young born to 13 pregnant females brought into the laboratory was 29 females to 28 males (Table 19).

(ii)Discussion

Changes in the population size over the three year period could be correlated with the length of the breeding season. Thus in the 1963/64 breeding season which was of average length, the population rose from 18 to 30 as the juveniles and sub-adults entered the trappable population. Then, during the following winter, it fell almost to the pre-breeding season level. During the long 1964/65

breeding season when animals continued breeding into the early winter, the population reached the maximum size recorded (40), and though numbers dropped during the late winter they did not fall to the pre-breeding season level. Consequently at the beginning of the 1965/66 breeding season the number of adults in the population was higher than in either of the two previous years. However the 1965/66 breeding season was short, lasting only until early February, and the population size dropped, so that at the beginning of the winter numbers were well below what they were at the beginning of the breeding season (Fig. 19).

As well as the length of the breeding season, changes in the survival rates of individuals in some sections of the population could be correlated with the population size changes. The high survival rates of juvenile males in February and March 1965 and of adult females during the 1965 breeding season (Section VIII) contributed to the large size of the population in 1965. Also the fall in numbers during the 1965/66 breeding season resulted as much from the low survival rates of the juveniles in this season and of the adult males in December 1965 and January 1966 (Section VIII), as from the shortness of the breeding season.

Both Newson (1963) and Krebs (1966) found a correlation between long breeding seasons and increasing populations in Clethrionomys glareolus and Microtus californicus respectively. At least in the older age groups, they also found a correlation between generally high survival rates and increasing population,

though, as mentioned elsewhere, Krebs found no clear relationship between early juvenile and "weanling" mortality and population changes.

The changes in survival rates though of short duration caused changes in the structure of the R. fuscipes population at Mt. Glorious between the years (Figs. 20 and 21). At the beginning of the winter, (June) in 1964, most of the animals in the population were juveniles and sub-adults recruited from the previous breeding season. Though the males of this year class, after breeding in the 1964/65 summer, dwindled in numbers during the following autumn, the female numbers remained high well into the 1965 winter (Fig. 20). Also during the 1964/65 breeding season a disproportionately large number of young males compared with young females were recruited into the population (Fig. 21). Thus in the winter of 1965, though most of the males in the population belonged to the 1964/65 year class, less than one half of the females did. However during the late winter many of the adult females disappeared, and by the beginning of the 1965/66 breeding season most of the animals were recruits from the previous breeding season (1964/65). Recruitment of young animals to the population from the 1965/66 breeding season was very poor. Due to this fact and the low survival rates of the adult males in December 1965 and January 1966 the number of males in the population in the autumn and early winter of 1966 was very low (Fig. 21). However in the spring and early summer of 1966 (September and December) new males (judged to be young adults of the 1965/66 year class from their body weights) entered the population

presumably from the area surrounding the grid. On the other hand adult females again survived well during the winter, and since few young females from the 1965/66 breeding season were recruited, the breeding population in December 1966 comprised mainly old females of the 1964/65 year class (Fig. 20).

What the variations in the length of the breeding season and mortality rates were due to was uncertain. There was no evidence in the results which could be interpreted along the lines of the latest models for population changes put forward by Chitty (1960) and Christian and Davis (1964). Predation and disease were not studied, and food supply was not critically studied, therefore what affects these factors had on mortality, and in the last case, on breeding were unknown.

Relatively steady population levels appear to be a feature of rat populations provided that the habitat remains relatively constant (Davis,1953). And though McDougall (1946b) noted population build ups and declines which lasted over several years for R. conatus, these changes occurred in sugar cane habitat where farming practices considerably influenced the quality of the habitat from time to time.

Relatively high numbers of transient females were associated with the end of the breeding season in 1964 and 1965 though in 1965 they were also as numerous in the population in March and April (the middle of the particularly long breeding season of this year) (Fig. 22). No transients were recorded during the 1963/64

breeding season.

Very little juvenile dispersal was recorded (Section VII), and it appeared that it was the adults which dispersed. The end of the breeding season when population pressure is greatest would therefore seem to be the natural time for an increase in the number of adult female transients. The number of female transients in the middle of the 1964/65 breeding season was perhaps related to the relatively large population which had built up at that time. This could have resulted in competition for suitable nest sites and disturbance of lactating females by other juveniles and sub-adults so that adult females were induced to move about in search of less crowded conditions (7 of the 10 female transients in March and April 1965 were adults).

The higher number of male compared with female transients during the study can be related to the more extensive movements made by the males than by the females (Section VII), particularly since many of the transients to the grid population were actually animals on "exploratory sallies" from areas in which they normally resided, well outside the grid.

The pattern of rising numbers of male transients in late spring and early summer correlated well with the commencement of the breeding season. All male animals in the population were fully mature at this time of year (Section VI) and the increase was almost certainly due to males searching for mates. Analysis of male movements (Section VII) showed that these were more extensive in the breeding season than in the nonbreeding season.

The sex ratio at birth was 50:50 (Table 19) and there was a general tendency for females to survive better than males. Thus, though the sex ratio in the population each month showed no statistically significant difference (except in June 1966 when females were more abundant - Table 18), the preponderance of male individuals in nearly all months, and the significant difference between the total number of adult males and females captured, needs explanation. Male movements were considerably larger than those of females (Section VII) except in the 1965 nonbreeding season. Observed home range lengths of males were also much greater than those of females. Males caught in a set of traps would thus be drawn from a much larger area than females and consequently more males than females would be caught. A similar conclusion was reached by Kikkawa (1964) when trapping Apodemus with widely spaced traps gave a high male to female sex ratio, though intensive trapping gave a slight excess of females, and he stated (p.269) "These results suggest that males were drawn from a larger area than females ..... Therefore, the sex ratio of trap catches in a given area may be biased".

The significant difference noted between the total number of juvenile males and females captured on the grid resulted from the large numbers of young males recruited in the 1964/65 breeding season. Considering only the juveniles of the previous and following seasons the sex ratio was almost 50:50 (15 females to 17 males), which was what would be expected from the evidence of the 50:50 sex ratio at birth recorded from the

pregnant females brought into the laboratory. None of these females were collected during the 1964/65 breeding season, so that whether the larger number of young males trapped in that season was due to a high male sex ratio in the newborn young, or to a lower survival of female nestlings in that year, was unknown. Juvenile females in the 1964/65 season did have a somewhat lower survival rate than the males (Table 11). On the average it would seem that the sex ratio of R. fuscipes in the field does not normally vary significantly from 50:50.

C. Melomys cervinipes

(i) Results

The population of M. cervinipes showed an increase in numbers during the autumn and winter followed by a fall during the spring/summer period (Fig. 19).

Owing to the difficulty of distinguishing between sub-adults and adults (See Section VI), and to the low number of juveniles trapped, the year classes graphed in Figure 25 have only been divided into males and females. A few juveniles were caught in November, about two months after the beginning of the breeding season, but most of the individuals of a particular year class were caught during the winter (Fig. 25). In the spring when breeding commenced (September/October) the trappable population fell relatively sharply. During the summer and the following winter adult numbers fell more slowly, and in both sexes a few survived to a second breeding season.

No useful analysis of the number of transients and residents in the population was possible owing to the poor trappability of this species.

The sex ratio of the total number of individuals of M. cervinipes captured on the grid was 55 males to 56 females. Six pregnant females brought into the laboratory gave birth to a total of 11 young, five

females and six males (Table 19).

(ii) Discussion

During 1963 and early 1964 trapping success was extremely poor, and though it improved during the rest of the study, captures of most individuals were so infrequent that interpretation of the data on population size and its fluctuations was very uncertain. However the results showed that the magnitude of the population fluctuations in the years 1964 - 1966 followed a similar sequence to those of R. fuscipes (Fig. 19). Also, as recorded for R. fuscipes, a prolonged breeding season preceded the occurrence in 1965 of the greatest numbers in the population. Further, in both species recruitment and the population level dropped significantly in the following year, 1966, and the breeding season was considerably shorter. It thus appeared that some factor or factors had affected the breeding similarly in both species. Unfortunately demographic data were insufficient in M. cervinipes to take this comparison further.

The small population size of M. cervinipes from about November through to April was due to a fall in adult numbers and the low numbers of young animals captured even though breeding had been in progress since September. Whether the fall in adult numbers was due to animals spending more of their time up in the trees than on the ground during the breeding season (the only nest of M. cervinipes found was 15 feet off the ground in an old hollow palm stump), or was due to mortality, was uncertain. The "tree trapping" programme gave insufficient data to help clarify the situation. The low number of juveniles which were captured appeared to be due to their reluctance to enter traps, since most of the new animals were caught as ? sub-adults or adults.

Since the new "recruits" to the population each year were not caught until after the R. fuscipes population had reached its yearly

peak and begun to fall (Fig. 19) it was thought that competition for traps might have occurred between these two species. However on examining the trap catches in April 1965 when the M. cervinipes population was low and the R. fuscipes population was high, and in September 1965 when the reverse situation occurred, it did not appear that competition for traps was the cause of the inverse population fluctuations in these two species. On the four trapping nights in April the usual number of 48 traps were set each night, and of these 32, 30, 29 and 42 traps were occupied by either R. fuscipes or A. stuartii. In September 32, 30, 28 and 27 traps were occupied by these two species out of the 48 set each night. Thus except for the last night in September the number of traps available for M. cervinipes was the same in the two months. Yet in April only four individuals were caught while in September 19 were caught, and though 12 were caught on the last night in September all but one were recaptures from earlier in the same month.

The sex ratio in M. cervinipes never varied from about 50:50 in any month, and the total number of males and females caught on the grid was equal in marked contrast to R. fuscipes and A. stuartii. However this was to be expected since the sex ratio at birth was 50:50 (Table 19), and the extent of male movements was not very much greater than that of females in contrast to the movement patterns of the other two species.

D. Antechinus stuartii

(i) Results

Each year the numbers of A. stuartii increased considerably during the late summer and autumn, and then fell during the late winter and spring to a late spring/early summer "low" (Fig. 19).

The season's young first entered the trappable population in February each year and their numbers increased up to June (Fig. 23).

From June onwards female numbers steadily declined up to September when they bred. After breeding their numbers further declined during the late summer and winter, but each year a few survived to breed a second time as two year old animals. The number of males on the other hand, fell after June, rose again in September, then "crashed" to zero in late September or very early October, so that from October to January each year the only males in the population were pouch young or young being suckled in a nest.

The number of transient individuals in the A. stuartii population from October 1963 to January 1966 was generally low (Fig. 24), particularly in the case of the females. Most of the female transients were caught during the breeding season. Some male transients occurred in the population during the winter, but in September the percentage was high (Fig. 24).

The sex ratio in the total A. stuartii population each month did not vary significantly from a 50:50 ratio if those months were ignored in which virtually no trappable male animals were present in the population (Table 20). However throughout the duration of the "grid trapping" many more males than females were caught (134 males : 85 females, $X^2 = 10.96$, 1 d.f., $P < 0.001$). Examination of the pouch young of six females showed a 50:50 sex ratio (Table 19).

(ii) Discussion

The yearly population fluctuations of A. stuartii on the trapping area were comparatively large, the numbers at the yearly peaks reaching three to five times those at the yearly lows (Fig. 19). The magnitude of the fluctuations were caused mainly by two factors:

1. The 100% mortality in the males each year at the end of September and

Table 20 The monthly sex ratios for the A. stuartii population and the results of X^2 tests (significant results underlined) between total numbers of females and males, and non parous females and males, using Yates' correction for continuity where the unadjusted X^2 was larger than the tabulated X^2 for P = 0.05.

Month	Total females	Non parous females	Total males	Total females and males X^2	Total females and males P	Non parous females and males X^2	Non parous females and males P
1963							
Sept.	13	13	16	0.31	>0.50	0.31	>0.50
Oct.	12	0	0	10.08	<0.005	---	---
Nov.	11	0	0	9.09	<0.005	---	---
Dec.	7	0	0	5.14	<0.02	---	---
1964							
Jan.	--	--	--	---	---	---	---
Feb.	8	2	10	0.22	>0.50	4.08	<0.05
Mar.	10	6	13	0.40	>0.50	2.56	>0.10
Apr.	--	--	--	---	---	---	---
May	16	12	18	0.11	>0.70	1.20	>0.20
June	21	17	27	0.75	>0.30	2.26	>0.10
July	20	16	19	0.02	>0.80	0.25	>0.50
Aug.	19	15	17	0.11	>0.70	0.12	>0.70
Sept.	17	14	29	3.13	>0.05	4.55	<0.05
Oct.	18	0	1	13.47	<0.005	---	---
Nov.	17	0	0	15.05	<0.005	---	---
Dec.	14	0	0	12.07	<0.005	---	---
1965							
Jan.	18	0	0	16.05	<0.005	---	---
Feb.	24	9	12	3.36	>0.05	0.42	>0.50
Mar.	19	5	16	0.02	>0.80	4.76	<0.05
Apr.	18	9	14	0.50	>0.30	1.08	>0.20
May	20	11	15	0.71	>0.30	0.60	>0.30
June	20	11	13	1.48	>0.20	0.16	>0.50
July	17	10	11	1.28	>0.20	0.04	>0.80
Aug.	11	7	6	1.46	>0.20	0.69	>0.30
Sept.	8	4	8	---	---	1.33	>0.20
Oct.	9	0	0	7.11	<0.01	---	---
Nov.	10	0	0	8.10	<0.005	---	---
Dec.	9	0	0	7.11	<0.01	---	---
1966							
Jan.	8	0	0	6.12	<0.02	---	---
Feb.	9	1	1	4.90	<0.05	---	---
Mar.	12	8	8	0.80	>0.30	---	---
Apr.	13	10	11	0.16	>0.70	0.04	>0.80
June	15	11	19	0.26	>0.50	2.13	>0.10
Sept.	7	6	12	1.31	>0.20	2.00	>0.10
Dec.	5	0	0	3.20	>0.05	---	---

2. A change in mobility of the males during each year in May and June.

The pattern of the fluctuations in 1964 and 1966 was similar and will be discussed together before interpreting the 1965 pattern. The unique male mortality in September has already been examined and its effect on the population size is clear. The effect of male mobility is discussed below.

Since females of A. stuartii produced only one litter a year, and breeding was synchronous throughout the population, all the season's young were weaned at the same time (February). It would therefore be expected that the population would increase during the following month or two (March and April) as the young animals entered the trappable population, and then would level off and in May commence to fall due to mortality factors.

However relatively large numbers of unmarked animals were caught in May and June in 1964 and in June 1966 so that the population continued to rise steeply in these months. As no breeding was taking place these unmarked animals must have either grown to a trappable size in June, or moved into the trapping area from outside, or changed their behaviour towards the traps.

It did not appear that they had recently grown to a trappable size, since their body weights were within the same range as those of the recaptured animals at the time (30g - 46g, males; 22g - 26g, females), and well above the weights at which young animals began to be captured in traps earlier in the year (22g - 26g, males; 15g - 20g, females). However it was significant in the light of the movement patterns (Section VII), that a large proportion of these unmarked animals were

males (19 males c.f. 8 females in 1964 and 10 males c.f. 4 females in 1966).

Male movements showed a statistically significant increase in size between the periods of March/April and May/June for 1964 and 1966, but female movements showed little difference between these two periods. This increase in mobility of male animals would increase the effective area with respect to males being sampled by the grid traps. In other words a larger male population would be being sampled in May and June than in March and April, and hence a rise in the estimated population would occur as observed. However a few of the unmarked animals caught in May and June may have been living on the trapping area and escaped being captured before May or later. This was particularly likely in the case of the females since their movements showed no marked change between the March/April and May/June periods.

The absence of a similar increase in the population during May and June 1965 seemed to be related to the high mortality of the young animals in that year (Section VIII). Presumably the high mortality recorded on the grid also occurred in the surrounding population, and so reduced their numbers by May that, though the mobility of the males increased as usual in the May/June period, only five unmarked males moved onto the grid. Further, the entry of these five animals into the estimated grid population was balanced by mortality among the other resident males, so that no increase at all was shown in the population estimates graphed in Figure 19.

The peak in numbers in September 1964 was due to a relatively large number of unmarked males (16) being captured during this month. Unmarked males were also caught in September in 1965 and 1966, but their numbers were much lower (5 and 6 respectively) than in 1964, and their

entry into the population was masked in Figure 19 by mortality among the other individuals during August in 1965, and by the absence of trapping data for July and August in 1966. Most of these new animals caught in September were transients (see below).

Thus the population fluctuations recorded for this species on the study area were due mainly to the unique mortality pattern of the males, together with a one litter a year breeding cycle which occurred simultaneously throughout the population. The highs in the population were exaggerated by the movement patterns of the males, combined with the small size of the sampling area. Over a larger area population figures would be steadier, though the pattern of high winter and low "unisex" summer numbers would, owing to the biology of the species, remain the same.

There was a marked difference in age structure of the population between 1964 and 1965. 1963/64 was a successful breeding season for the species with a good recruitment of young into the population (Fig. 23). A few postbreeding adult females survived into the winter, but only two were still alive and bred again in the 1964/65 season. The number of young recruited to the population from the 1964/65 breeding season was well below the previous year's level, even though there were more breeding females present, 18 in October 1964 compared with 12 in 1963. Many postbreeding adult females lived on into the winter months, and six bred again in the 1965/66 season, while only four young females survived to breed that year. What factors were effective in bringing about this difference in recruitment between 1964 and 1965 were uncertain, but four points seem to be worth noting in this respect.

1. The number of young born per female was about the same in both seasons (7.4 young/female in 1963/64; 7.8 young/female in 1964/65). Pouch mortality was also relatively similar (0 in

1963/64 and 0.39 young/female in 1964/65). Therefore low fecundity was not the cause of the low recruitment.

2. At the time the 1963/64 young were being weaned (February) in 1964 only five adult females were present in the "grid" population. However in February 1965 fifteen adult females were present, and this number did not drop until April and then only to ten. Thus in 1965 the young may have had difficulty establishing themselves in the population in the face of the unusually large numbers of adults present. The survival rate of both the male and female young animals between February and March was very low in 1965 compared with the preceding and following years (Tables 15 and 16). The high survival rate of the adult females was not accounted for.

3. 1965 was a drought year throughout Queensland, and at Mt. Glorious the rainfall dropped from an average of 64 inches (163 cm) per year in 1962, 1963 and 1964 (Fig. 2) to 40 inches (102 cm) in 1965 if the downpour on July 8th (see below) is discounted in the average. Instead of the usual monthly peak of rainfall in March a "low" occurred (Fig. 2). The litter of the forest floor was very dry and cracks appeared in the soil. This would drastically affect the invertebrate fauna in the litter, a major source of food for this insectivorous species. Thus not only were the young faced with a comparatively large adult population, but almost certainly a food shortage.

4. On the night of July 8th 1965 a cyclone passed down the Queensland coast near Brisbane and $8\frac{3}{4}$ inches (22 cm) of rain fell during that one night at Mt. Glorious. A sharp drop in the survival rate between July and August occurred in the young males, and a less sharp drop in the adult and young females (Tables 15 and 16). It seems possible that such a downpour could have had a direct effect on the survival

of a small animal such as A. stuartii.

A comparison of the 1965/66 breeding season with that of 1964/65 shows that the number of females at the start of the season was only one half the number at the start of the 1964/65 season. Notwithstanding this, the population reached the same level in the winter of 1966 as it did in 1965, and this despite the fact that 1966 was another very dry year at Mt. Glorious (Fig. 2). However the number of adult females in the population at weaning time (February) was only one half the number in 1965, and by April only three remained compared with 10 in 1965. In the 1965/66 breeding season the number of young born per female, and the number of young lost during pouch life per female - 7.6 and 0.33 respectively, were the same as in the 1964/65 season - 7.8 and 0.39. Thus the recruitment of young in 1966 pointed to the suggestion that the number of adult females in the postbreeding population was the important factor in relation to the successful recruitment of young into the population.

The low number of transients recorded in the A. stuartii population (Fig. 24) suggests relatively strong site attachment in this species, and agrees with the finding that very few individuals undertook dispersal movements. The relatively high percentage of female transients in December 1963 and February 1964 (Fig. 24) was due to the small number of animals captured at these times. Only three transient individuals were involved, one in December and two in February. As in R. fuscipes the percentage of male transients was highest at the start of the breeding season. These September transients were presumably animals roaming widely in search of mates. However even these animals did not appear to be wandering at random through the forest. The capture records of many of them indicated that their extensive movements were in the nature of "exploratory sallies" (in search of mates) since they returned at times

to their previous home range area (see Fig. 11 for examples). In fact most of the animals recorded as transients would seem to have been on "exploratory sallies". During 1965, when the line traps were being operated, four female and eight male transients were recorded in the "grid" population. Three of these females (75%), and six of the males (75%), were known from their capture records to be resident on the lines both before, and after, their temporary appearance on the grid. Thus it would seem that extremely few "migrant" individuals occurred in the A. stuartii population at Mt. Glorious.

The anomalous situation of more females present in the population in many months of the year (Table 20), though throughout the year more individual males were caught, was a result of the much longer life span of the female animals. When a comparison was made between the number of males and females of the same age present in any particular month, the males were more abundant than the females. However the difference was only statistically significant in February and September 1964 and March 1965 (Table 20). In February 1964 the difference was explained by the fact that the newly weaned males started to be captured before the young females, though why this was so was unexplained as it did not occur in other years. The difference in September 1964 could be attributed to the large number of transient males in the population during that month. The significantly higher male sex ratio in March 1965 seemed to be correlated with a lower survival rate in the young females compared with the males between February and March (Tables 15 and 16).

Throughout the period of February to early September in each year the survival rate of the males if anything was lower than that of the females (Table 14), therefore some factor other than a differential survival rate

of weaned animals must be sought to account for the overall greater numbers of males than females, of the same age, which were caught on the grid. Since a 50:50 sex ratio was observed in the few pouch young examined (Table 19), a differential sex ratio at birth did not seem to be the cause. No information was obtained on the relative survival rates of males and females during the long nursing period of the young, so that a differential survival rate during this period remained a possibility.

However, the more extensive movement patterns of the males compared with those of the females, from the time the animals first started entering the traps (Table 9), pointed to the fact that the males were being drawn from a larger area around the grid than were the females, resulting in a bias of trap catches towards males as discussed above for R. fuscipes.

Thus, out of each age class more males than females were caught owing to the larger movement patterns of the males, and this resulted in the high percentage of males in the total number of individuals caught. But because of the much greater longevity of the females compared with the males, which resulted in a considerable overlap of female age classes (no overlap occurring in the male population from one generation to the next), often more females than males were 'known to be alive' in any particular month.

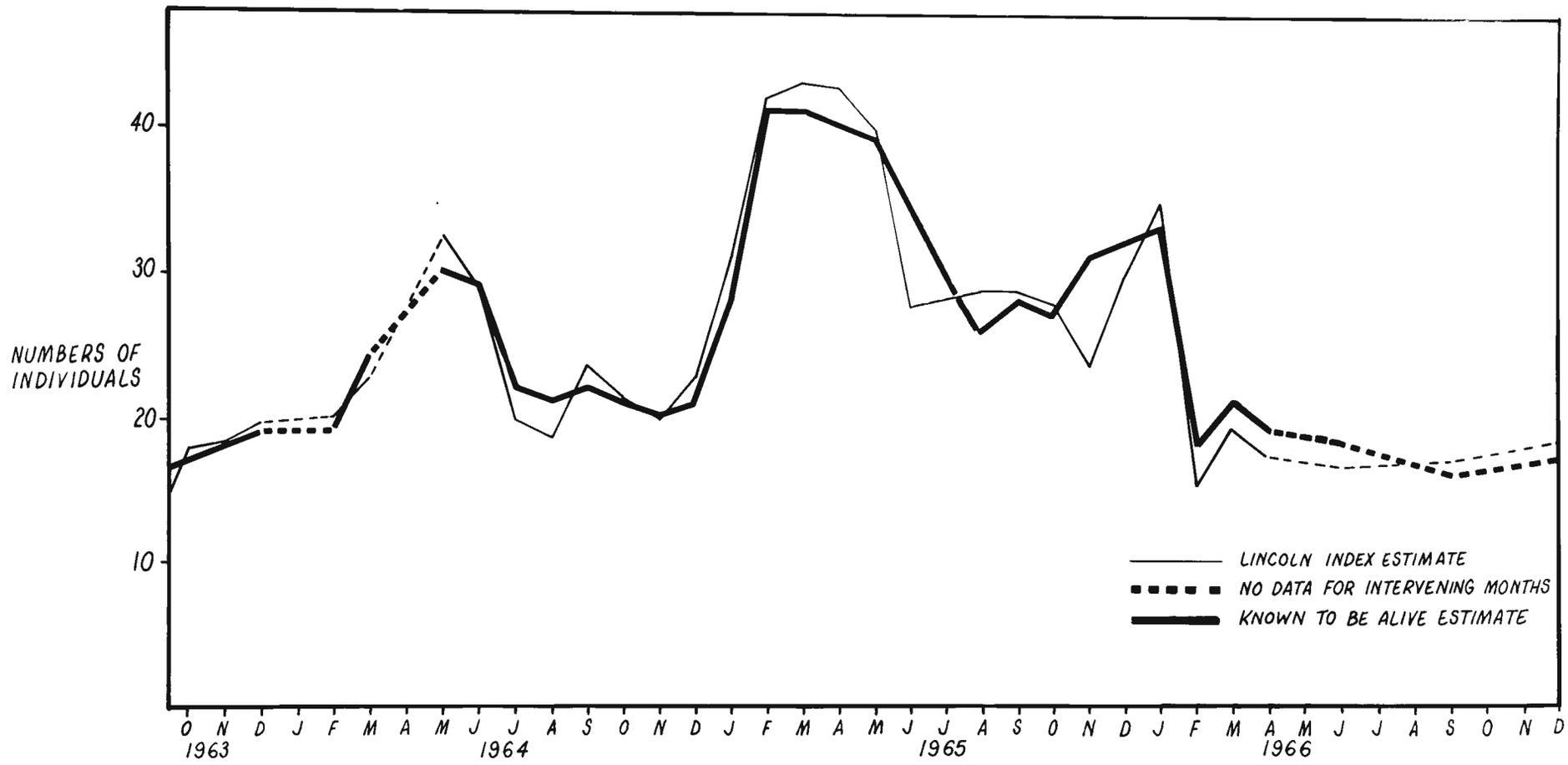


FIG. 16 POPULATION ESTIMATES OF R. FUSCIPES.

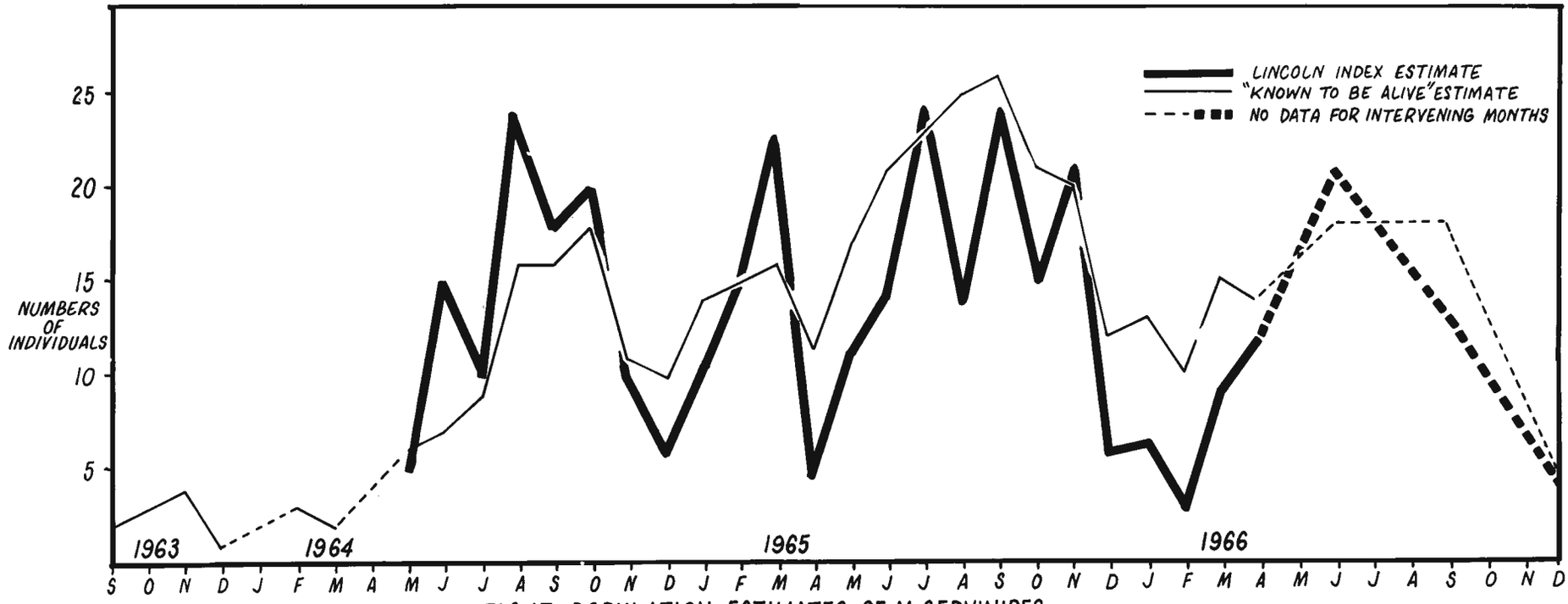


FIG.17 POPULATION ESTIMATES OF M.CERVINIPES.

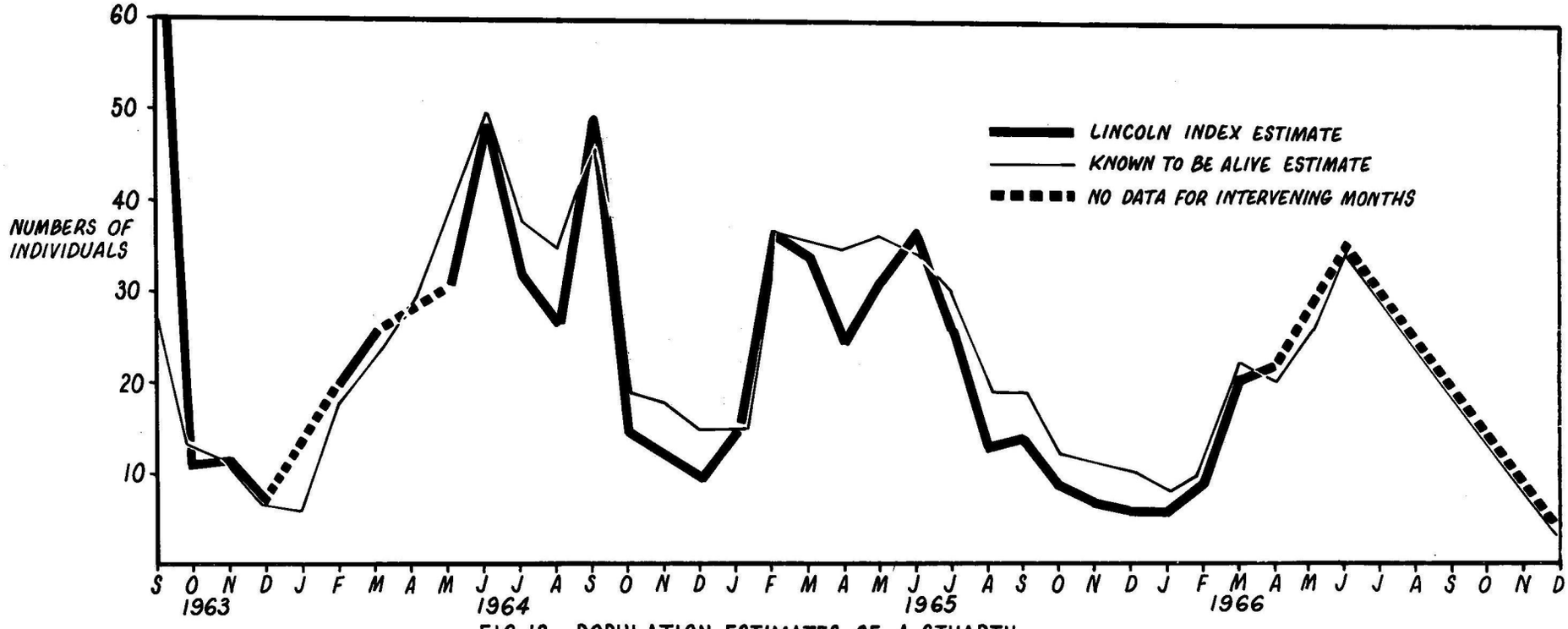


FIG. 18 POPULATION ESTIMATES OF A. STUARTII

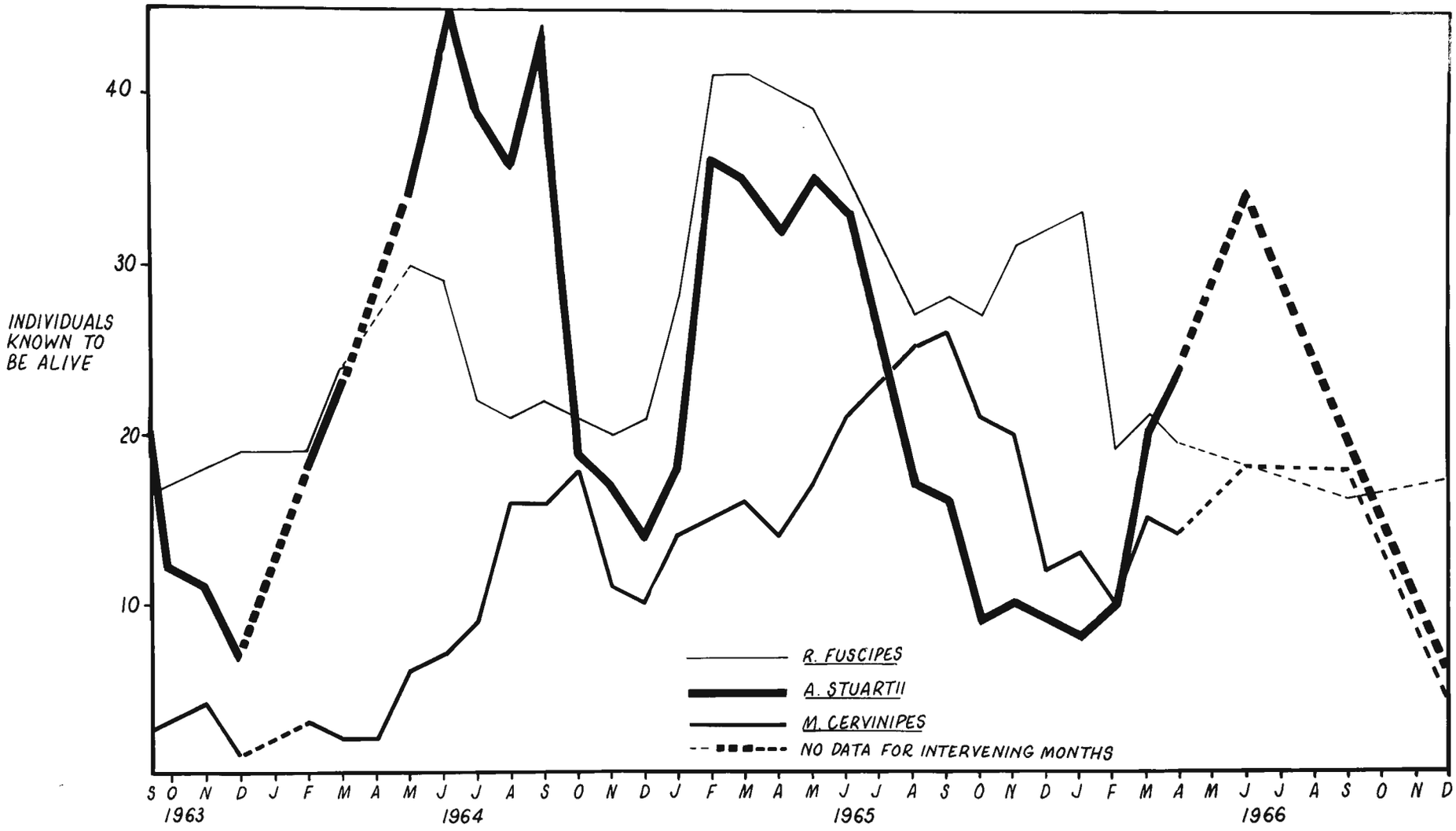


FIG. 19 POPULATION TRENDS IN R.FUSCIPES, A.STUARTII & M.CERVANIPES.

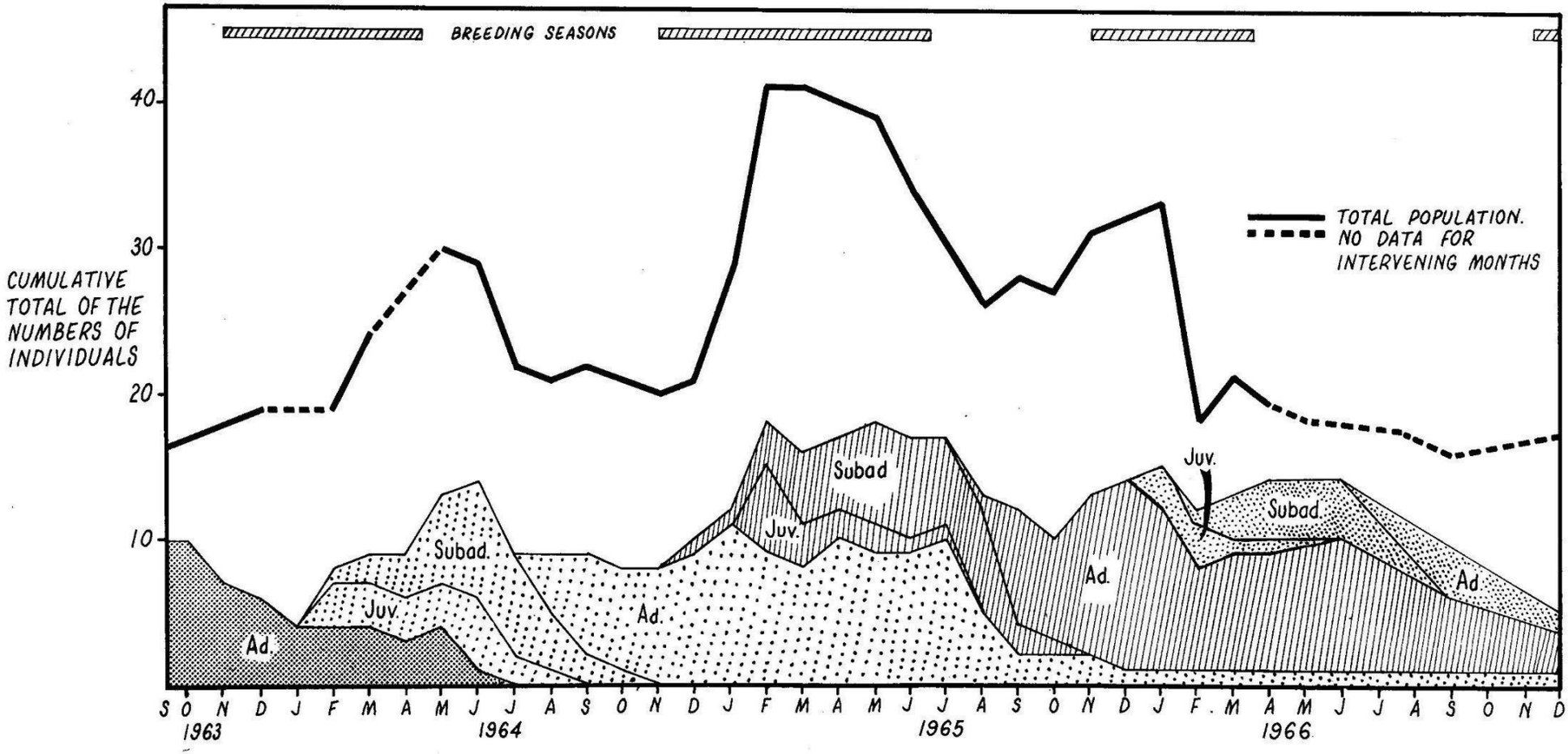


FIG. 20 YEAR CLASSES IN THE FEMALE R. FUSCIPES POPULATION.

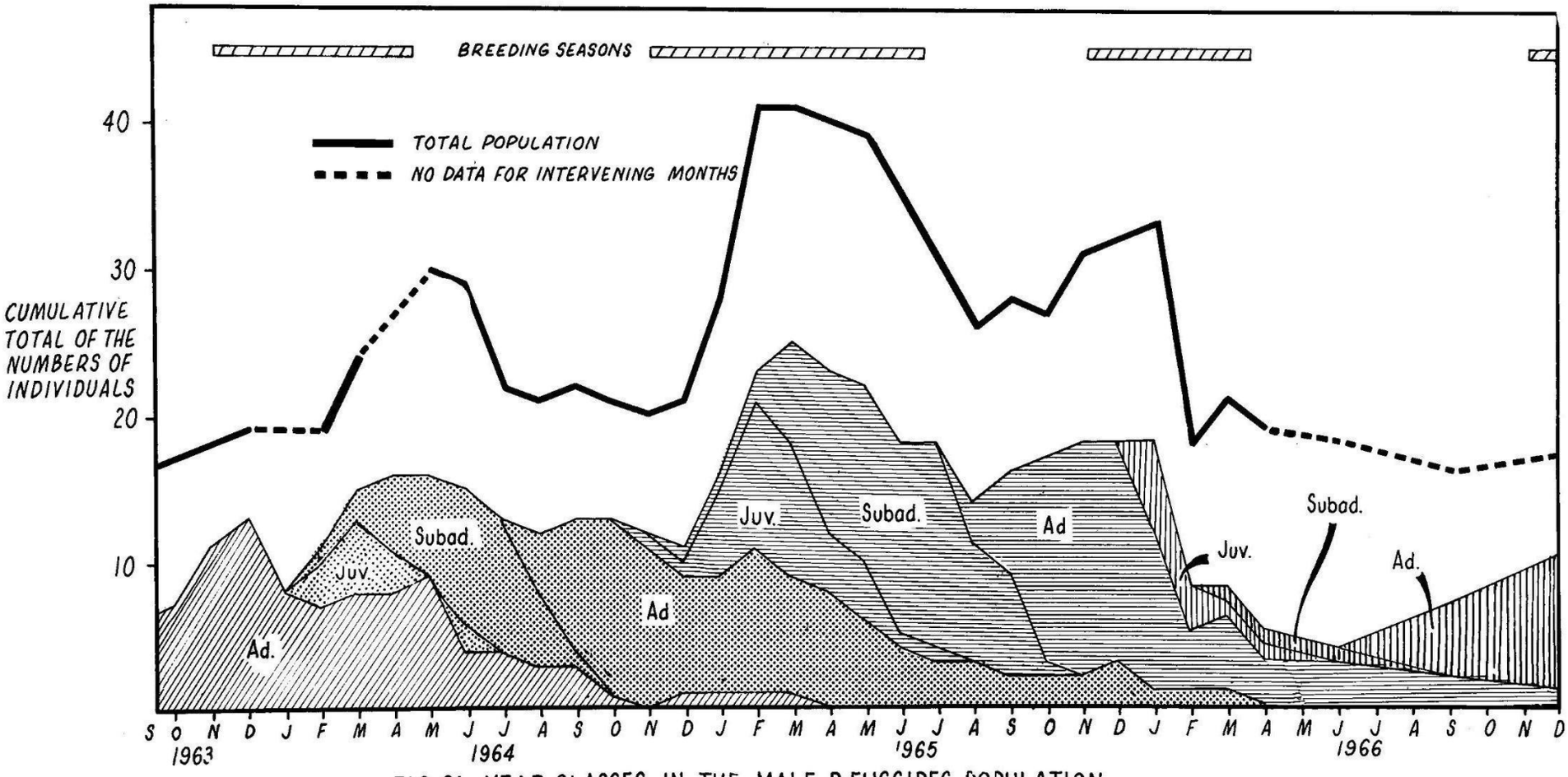


FIG. 21 YEAR CLASSES IN THE MALE R.FUSCIPES POPULATION.

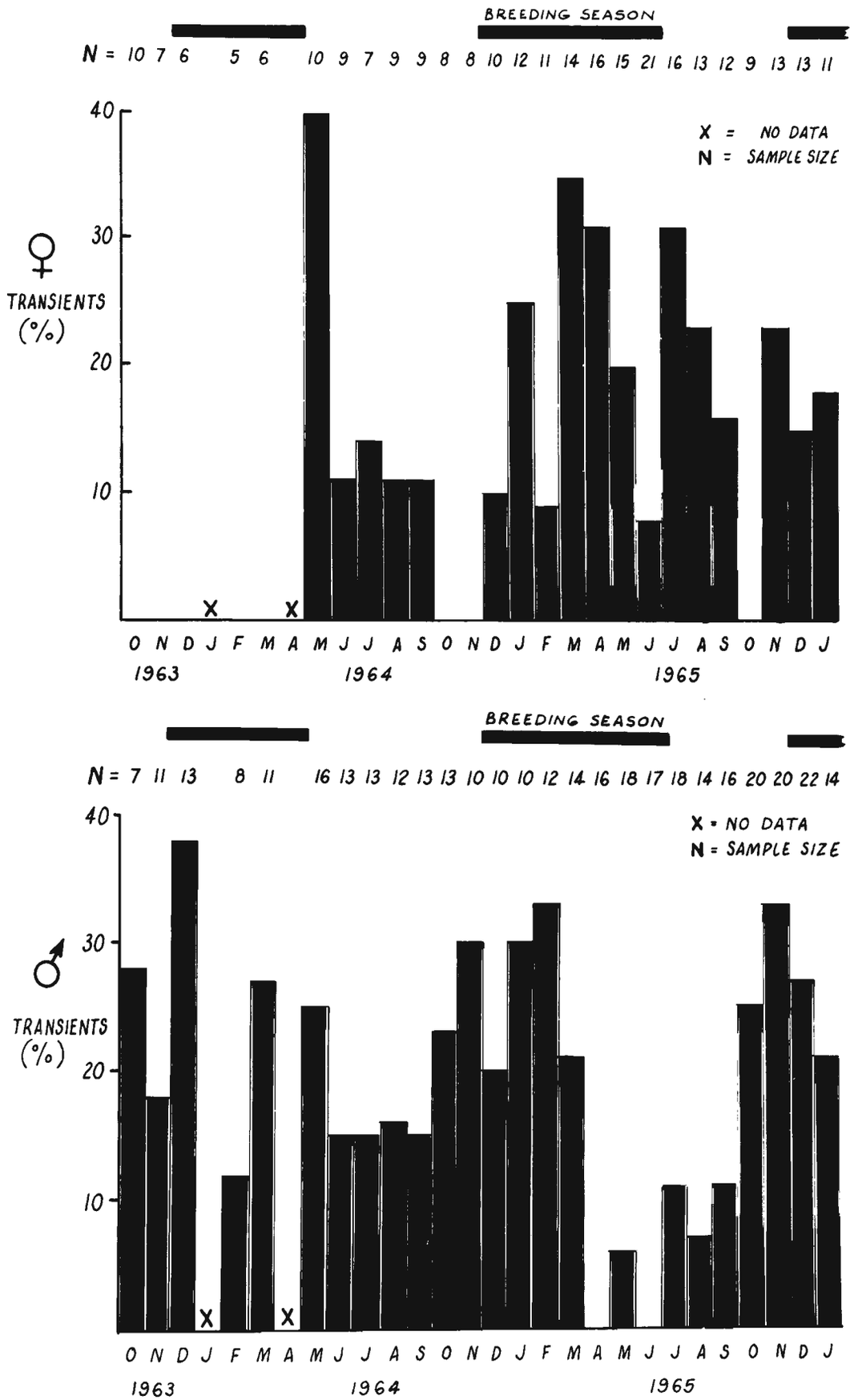


FIG. 22 PERCENTAGE OF FEMALE & MALE TRANSIENTS IN THE R. FUSCIPES POPULATION EACH MONTH.

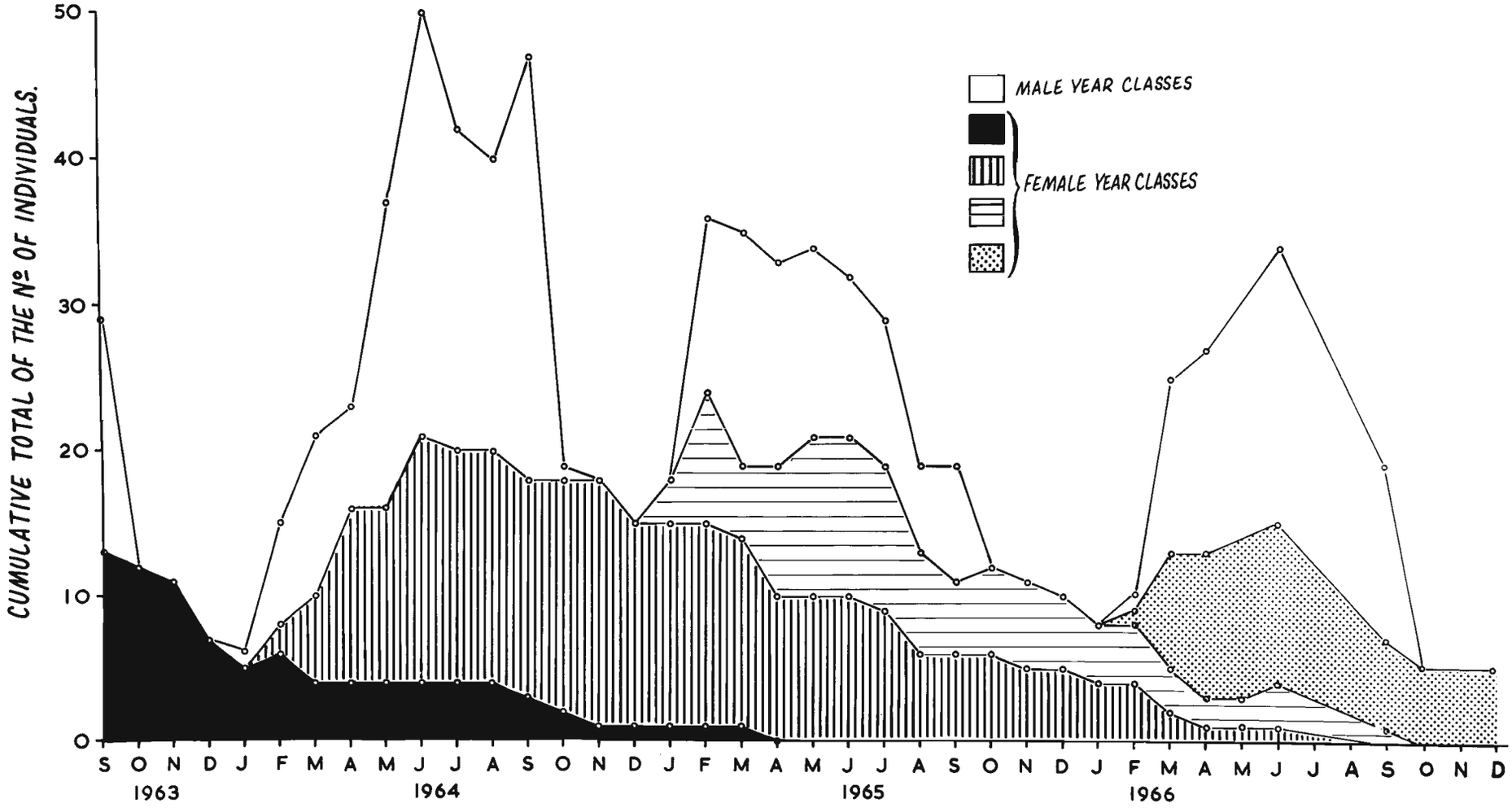


FIG. 23 YEAR CLASSES IN THE A. STUARTII POPULATION.

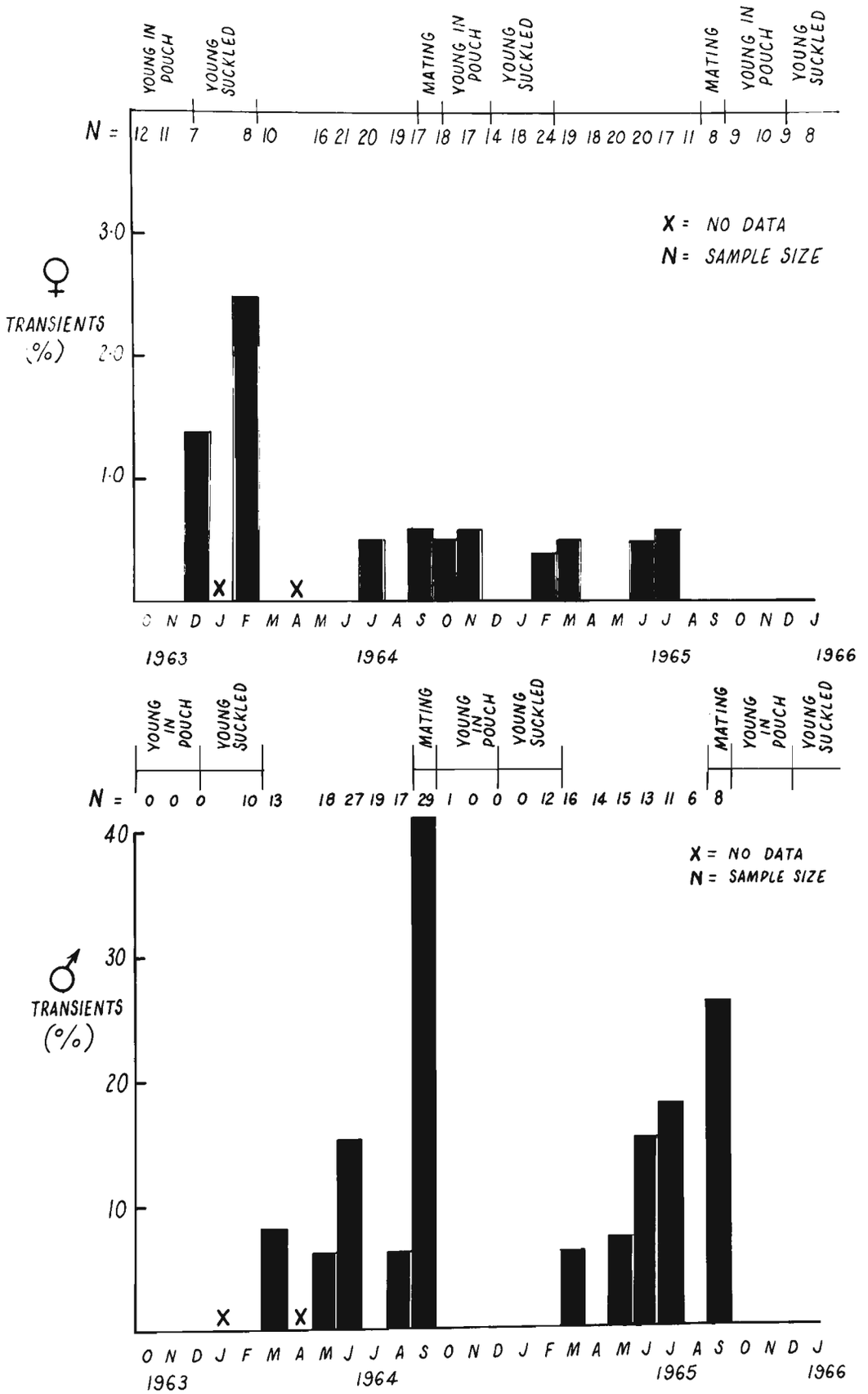


FIG. 24 PERCENTAGE OF FEMALE & MALE TRANSIENTS IN THE A. STUARTII POPULATION EACH MONTH.

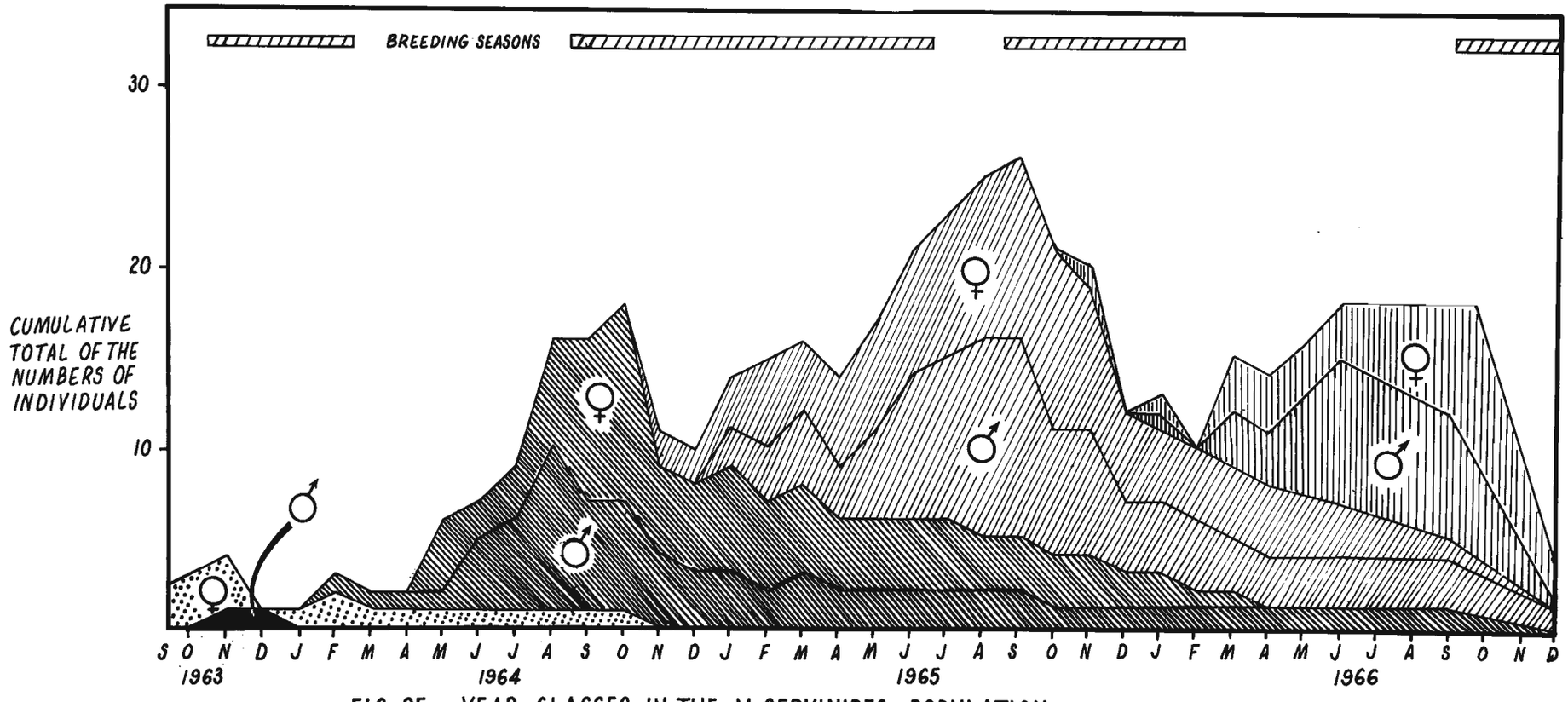


FIG. 25 YEAR CLASSES IN THE M. CERVINIPES POPULATION.

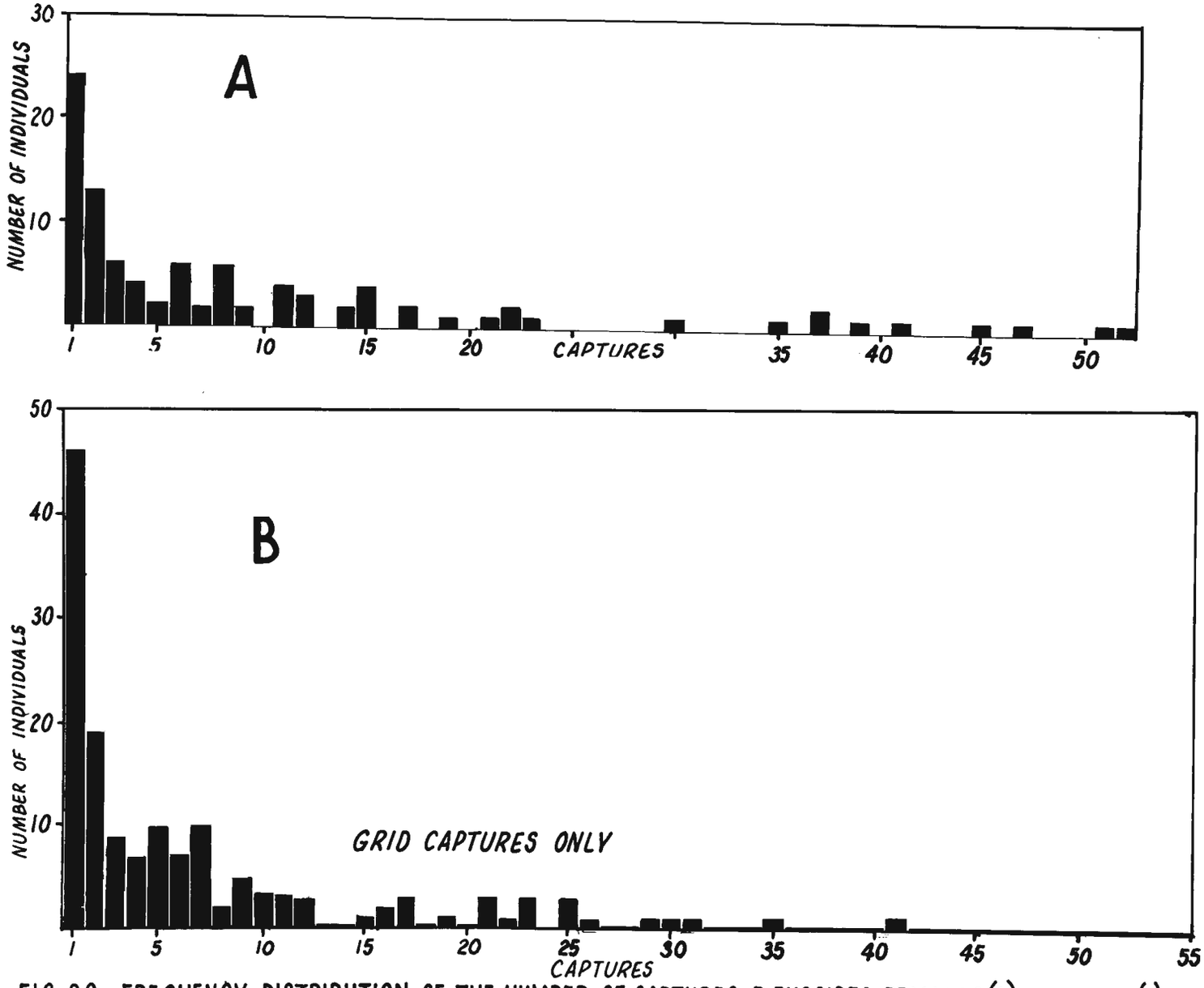


FIG. 26 FREQUENCY DISTRIBUTION OF THE NUMBER OF CAPTURES, R. FUSCIPES FEMALES (A) & MALES (B).

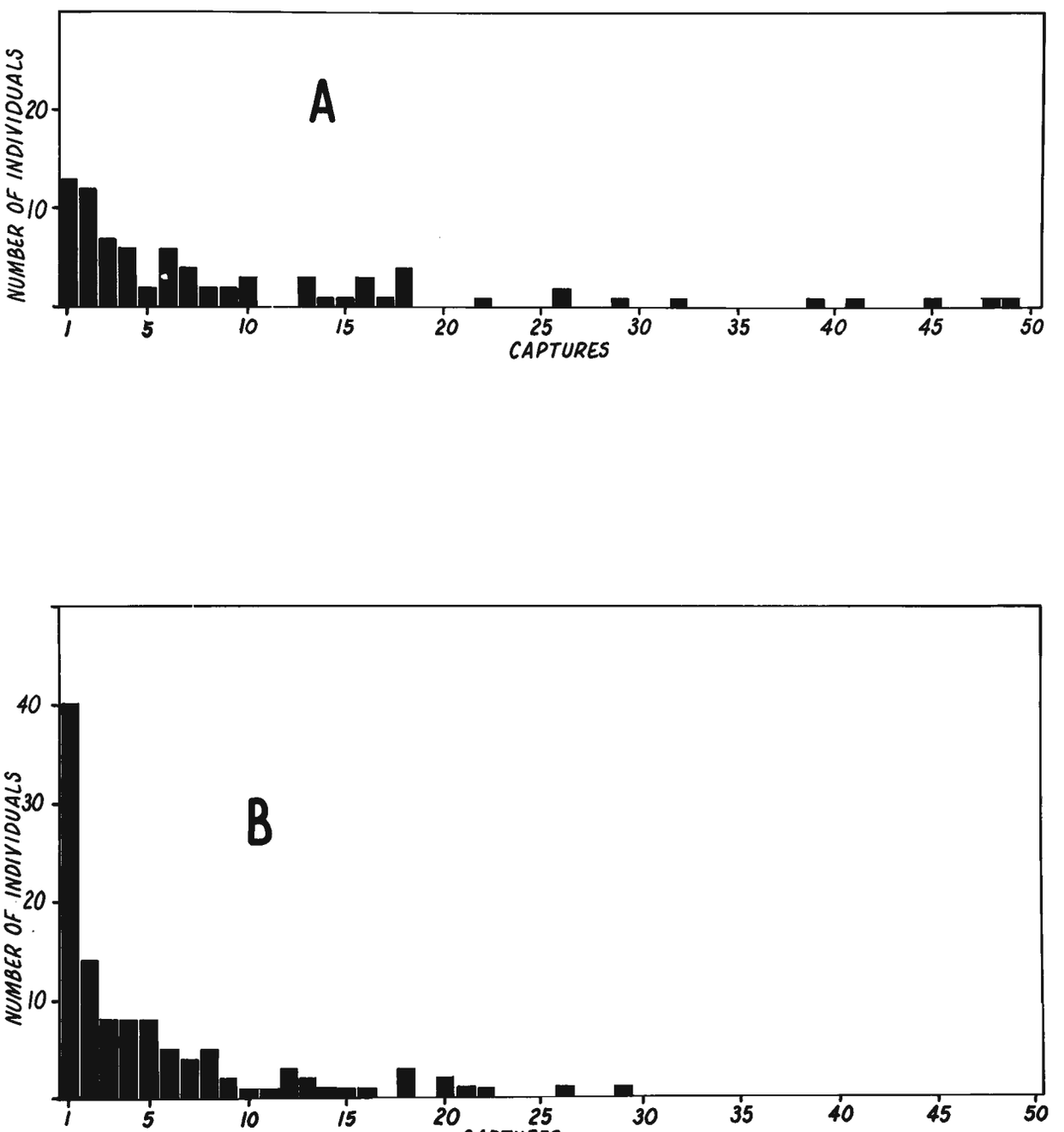


FIG. 27 FEQUENCY DISTRIBUTION OF THE NUMBER OF CAPTURES, A.STUARTII FEMALES (A), MALES (B). GRID CAPTURES ONLY.

X HABITAT UTILISATION

A. Periodicity in activity

(i) Methods

The activity patterns of the three species were investigated by trapping (see Section III). Traps were first set at 11.00 hours and cleared every three hours during the following 24 hour period. An assessment of the cloud cover during the night was made. The phase of the moon and the time at which it rose and set were obtained, and the time of sunrise and sunset was noted. During the activity trapping sequence rain, intermittent showers, fell only on one night, December 17th.

(ii) Results

The trapping results and meteorological data are presented in Figure 28.

R. fuscipes showed continual activity throughout the hours of darkness at all times of the year, but none during daylight. There was no marked peak in activity at dusk, or any other time during the night; in fact the most striking feature of the activity was its evenness and constancy. Usually many individuals were caught several times during any particular night.

Few individuals of M. cervinipes were captured. However in September, the month in which the highest numbers were trapped, there was a tendency for greater activity during the early part of the night. Further analysis of its activity pattern was not possible.

Activity in A. stuartii was not wholly nocturnal, as in the two

rodent species, except in December, when very few catches were made. There was a marked tendency throughout the year for a peak of activity at dusk, and in March and December there was also a second peak in activity at dawn, with a lull during the middle of the night. In June and September no dawn peak was apparent, and activity throughout the night was constantly high.

(iii) Discussion

As pointed out by Miller (1955) two main factors contribute to periodic activity in small mammals. An animal first satisfies its food requirements, thereby setting up a feeding rhythm, after which the animals preference for day or night may set up a secondary diel rhythm. The feeding rhythm in nocturnal animals usually results in a dusk peak of activity followed by a second peak sometime before dawn. In Apodemus sylvaticus such bimodality has been related to the fact that the volume of food which an animal needs during a 24 hour period is twice the capacity of its stomach (Elton et al 1931). Thus during the dusk peak of activity the stomach is filled; activity then falls off until the digestive processes empty the stomach causing "hunger pangs" which initiate a second peak of activity.

These basic rhythms may be modified by several other factors, important among which are day length (Miller 1955), interspecific relationships (Brown 1956) and food supply (Chitty and Shorten 1946).

The absence of peaks in the activity of R. fuscipes seemed unusual for a species so markedly nocturnal. Though Chitty and Shorten (1946) experimentally produced a dusk peak in the feeding rate at a baiting station in wild R. norvegicus, when food had been in relatively short supply for the previous week or so, when food was constantly in excess

a very even feeding rate throughout the night was maintained by the rats. Whether food was in excess for R. fuscipes at Mt. Glorious was uncertain.

The repeated capture of many individuals of R. fuscipes throughout the night suggested that rest periods if taken were of short duration, at least not long enough to be detected by the three hour trapping periodicity. The use of a portable radioactive ore detector (which produced clicks in a set of earphones that could be recorded on tape), placed over the nest site of a non-breeding adult female rat tagged with Tantalum 182, showed that,on seven different nights in April and May, the animal left its hole at dusk,and did not return until just before dawn. Thus if any rest periods occurred,they were not taken in the permanent daytime nest site. Attempts to obtain activity data for M. cervinipes and A. stuartii by the same method were unsuccessful.

Activity in A. stuartii was not limited to the hours of darkness, though a dusk peak in activity, the suggested mark of a nocturnal animal, was constantly observed. Smaller animals in general, particularly insectivores, seem to maintain a shorter feeding periodicity (Crowcroft 1954). It seemed therefore that A. stuartii individuals were by preference nocturnal, but their energy requirements necessitated some daylight feeding activity.

The constant level of activity throughout the night,which occurred in June after the dusk peak,also may have been related to food requirements. As evidenced by the cessation of growth through the winter, it would seem food supplies were minimal at that time of year. This would necessitate more time spent foraging,and result in a more constant level of activity throughout the night. In September the all night activity seemed likely to be related to breeding behaviour, since the short mating period occurred in this month.

Absence of a dawn peak in activity in both June and September could probably be attributed to the above disruptive factors on a basically bimodal feeding activity pattern.

Apart from any nocturnal preference in A. stuartii, an increase in activity at dusk must be of direct advantage to the animals, since an increase in insect activity was very noticeable in the forest just at dark.

The change in day-length between summer and winter was approximately three hours. The only noticeable change in the activity of any of the species that could be attributed to this relatively small difference was the slightly shorter duration of activity in R. fuscipes in December. In this month the sun rose just before the five o'clock visit to the traps, and no individuals were caught after this hour. In March, June, and September, when the sun did not rise till six o'clock or later, a few individuals were still active after the five o'clock trap round.

MacMillen (1964) has noted that moonlight did not affect the activity of rodents living in the five feet high scrub of the semidesert of Southern California in contrast to its effect in the nearby sparsely vegetated deserts. The canopy of the rainforest severely restricted the penetration of moonlight to the forest floor. Thus it was not surprising that moonlight had no effect on the pattern or degree of activity of R. fuscipes and A. stuartii, as was shown by a comparison of the night of March 9th, when the moon was just past the full and there was little cloud, with the night of March 11th, when heavy cloud completely cut out the moonlight.

There did not appear to be any interspecific influences on activity. The changes which occurred in the activity rhythm of A. stuartii, at least between March and June, did so while no apparent change took place in the

pattern of activity or the population size of R. fuscipes. It was not possible to assess any effects of M. cervinipes.

B. Arboreal activity

(i) Methods

"Tree trapping" was carried out once a month from March 1966 to February 1967 except for October 1966 in which month no "tree traps" were set. Nine traps were set at a height of 15 ft. (4.5 m) on small trees of the understory, and nine traps were set at the same height on large trees of the canopy. In addition, on a third night, eleven traps were set on a large "strangling" fig tree (Ficus watkinsiana), two at 10 ft. (3m), 20 ft (6 m), 30 ft. (9 m) and 40 ft. (12 m) heights on the trunk, and one at 60 ft. (18 m), 70 ft. (21 m), and 80 ft. (24 m) heights, and about 5 ft. (1.5 m) out along the branches of the Podocarpus elatus around which the fig was growing. The nine small trees of the understory (d.b.h. < 6 ins. (< 15 cm)), on which traps were set, were relatively evenly spaced out over an area of 100 ft. x 100 ft. (30.5 m x 30.5 m) towards one end of the trapping grid. The nine large trees of the canopy (d.b.h. > 2 ft. (> 61 cm)) used, were spaced out over a similar area just outside the edge of the grid about 200 ft. (61 m) from the small trees. The fig tree (F. watkinsiana) on which traps were set up to a height of 80 ft. (24 m) was also used as one of the group of nine large trees.

Both large and small trees were trapped on the same nights for two consecutive nights. On the following night eleven traps were set on the fig tree. Captures made on this night are analysed separately except in the seasonal analysis of the captures.

(ii) Results

The tree species and number of animals captured during the years trapping sequence are given in Table 21 and 22. The trunks of some of

Table 21 The species of small and large trees on which traps were set and the total number of animals caught. (+ = tree trunks covered with vines and creepers, - = tree trunks clean).

Size	Species	Trunk cover	R. fuscipes	M. cervinipes	A. stuartii
Small	Archontophoenix cunninghamiana	+	0	2	6
	Sloanea woolsii	-	0	1	3
	Argyrodendron actinophyllum	+	0	3	4
	Laportea gigas	-	0	0	2
	Penantia cunninghamii	-	1	4	4
	Beilschmedia obtusifolia	-	0	2	4
	Chrysophyllum pruniferum	-	0	1	6
	Diospyros pentamera	+	0	3	4
	Pseudocarpa nitidula	-	0	0	2
Total			1	16	35
Large	Archontophoenix cunninghamiana	-	0	0	0
	Sloanea woolsii	+	0	2	5
	Argyrodendron actinophyllum	+	0	7	6
	Laportea gigas	-	0	0	4
	Penantia cunninghamii	-	0	1	6
	Cryptocaria erythroxylon	-	0	0	5
	Eugenia corinantha	+	0	1	1
	Littsea reticulata	-	0	0	9
	Ficus watkinsiana	-	0	1	3
Total			0	12	39

the trees were covered with vines and creepers, and this is also recorded in Table 21. The seasonal distribution of all captures on trees is given in Table 23.

Table 22 Heights of captures on Ficus watkinsiana

Height (feet)	R. fuscipes	M. cervinipes	A. stuartii
10	3	3	7
20		3	7
30			5
40			5
60			0
70			0
80			2
Total	3	6	26

Table 23 Seasonal distribution of all captures on trees.

	Mar.	Apr.	May	June	July	Aug.	Sept.	Nov.	Dec.	Jan.	Feb.	Total
R. assimilis		1			1		2					4
M. cervinipes	3	3	3	2	2	1	6	3	2	7	2	34
A. stuartii	8	14	25	28	8	10	1	2	1	0	3	100

Four main facts are evident in the results.

1. M. cervinipes and A. stuartii show a marked degree of arboreal activity but R. fuscipes does not.

2. There was no difference in either M. cervinipes or A. stuartii between the amount of overall activity in the small and the large trees (Table 21).

3. A. stuartii showed a seasonal change in the degree of its arboreal activity (Table 23).

4. The activity of A. stuartii extends well up into the canopy (Table 22).

(iii) Discussion

R. fuscipes obviously makes little use of the arboreal part of the habitat and is truly a rat of the forest floor. The data shows also that A. stuartii is much more active in the trees than M. cervinipes. However the biological significance of this result was doubtful. The low trappability of M. cervinipes throughout the study, suggesting trap shyness, compared with the easily trapped A. stuartii, and, because of this, the uncertainty of the relative abundance of these two species, were both unknown variables of importance in assessing the comparative significance of the "tree trapping" results.

M. cervinipes showed more activity on "creeper covered" trees than "clean" trees (Table 21) when the relative number of these two tree "types" which had traps on them was taken into account. A. stuartii captures were about evenly distributed between the two types. The difference in usage of "creeper covered" and "clean" trees by M. cervinipes was highly significant, P = 0.0041 (median test with the Fisher exact probability test, Siegel 1956).

Further, if the "clean" trees are divided into the two groups large and small, and the "creeper covered" trees likewise (Table 24), it can be seen that M. cervinipes frequents the small "clean" trees much more than the large ones. However, the samples were too small to show statistical significance, X^2 = 2.50, 1 d.f., P>0.10 (using Yates' correction for continuity).

Table 24. Number of captures in large and small, "clean" and "creeper covered" trees. (N = number of trees).

	Clean		Creeper Covered	
	Large (N=6)	Small (N=6)	Large (N=3)	Small (N=3)
A. stuartii	27	21	12	14
M. cervinipes	2	8	10	8

A. stuartii showed no preferences for a particular type of tree, and M. cervinipes showed none with respect to large and small "creeper covered" trees.

The biological significance of these findings was twofold. M. cervinipes was a browser of leaves and shoots, and these were not easily reached on the larger trees whose "clean" trunks may rise 50 - 60 ft. (15 - 18 m) without bearing branches. In the smaller trees, and in large trees with trunks covered with creepers and other epiphytes, their food was more easily obtained. On the other hand, insects, the food of A. stuartii, can be found on the trunks and branches of all trees.

Secondly, M. cervinipes individuals, though they can climb among vines and small branches with agility, they are not adapted to run up and down relatively smooth flat surfaces such as the clean trunks of the larger trees. A. stuartii however is well adapted for scansorial activity (Wakefield and Warneke 1966), and individuals climb up or down smooth tree trunks with great speed, and seem to experience little trouble running upside down under large branches or steeply leaning trees (personal observation).

No seasonal change in arboreal activity was apparent in M. cervinipes. The seasonal variation in the arboreal activity of A. stuartii was almost directly related to the seasonal population changes. From the beginning of November to February the A. stuartii population is low comprising only adult females. In February the young are weaned, and the population rises to a winter maximum from which it falls irregularly until the "crash" at the end of September (Section IX). Arboreal activity followed the same trends (Table 23). The low numbers caught on trees in September was due to the fact that trapping was carried out at the end of

each month, and the male "crash" had already occurred by the time of the September "tree trapping".

The captures of R. fuscipes on the fig tree at a height of 10 ft. (3 m) can be explained by the fact that the tree leaned at a considerable angle, so that to reach the lowest traps no climbing ability was required.

The six M. cervinipes capture records on the fig tree form an interesting group of captures in view of the previous evidence that their use of large "clean" trees is limited. The six captures occurred over the period from August to February. The same adult male and female were caught twice each over this period. In February two juveniles and the adult female were caught on the same night. These records are highly suggestive that males and females form pairs, which fact was speculated on in the section on movements, and that they had a nest somewhere amongst the network of cable like roots which formed the trunk of the fig tree surrounding the host tree.

A. stuartii made extensive use of the fig tree, particularly in the winter (June and July), when seven and five individuals were caught in the one night's trapping in each of these months. The height to which A. stuartii went on this tree may not be representative of the height to which it went on other species. Fig trees are emergents in the forest, and even at 80 ft. (24 m) the trunk was large (2 - 3 ft. (61 - 91 cm) in diameter), and extended for a further 20 ft. (6 m) or more before it forked extensively into large spreading branches above the general level of the upper canopy.

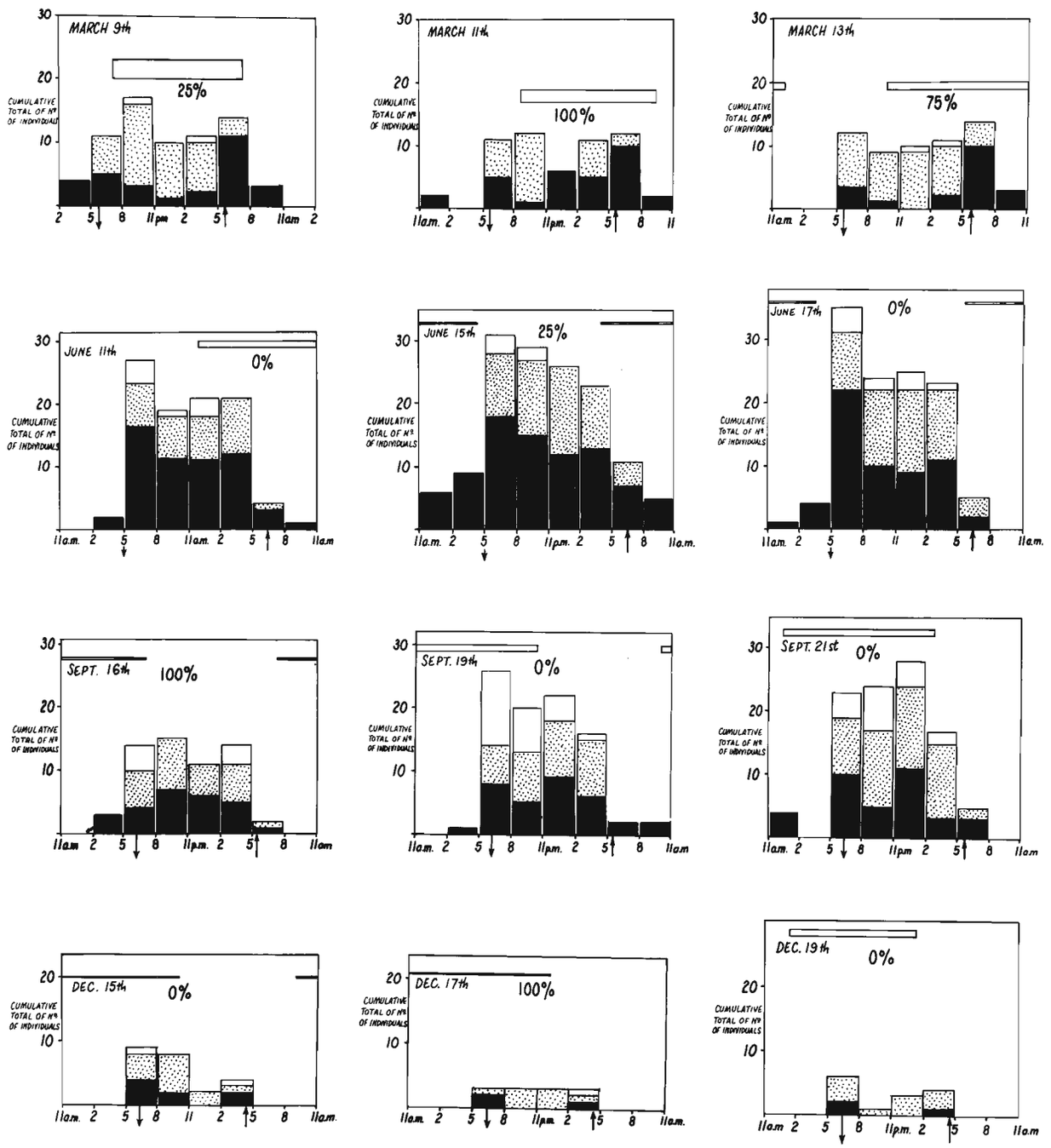


FIG. 28 PERIODICITY OF ACTIVITY AS REVEALED BY 24 HOUR TRAPPING PERIODS (METEOROLOGICAL DATA ALSO SHOWN).

XI COMPARISON WITH TEMPERATE AND TROPICAL SPECIES

The three species comprising the small mammal population at Mt. Glorious showed, in their general biology, some features similar to small mammals in temperate regions such as England, and others to small mammals in the tropics e.g. Malaya. Even though the subtropical rainforest habitat at Mt. Glorious was comparatively similar in structure to the tropical rainforest in Malaya, and very different from English woodland, in the main the relationship of the general biology of the small mammals was more with English than Malayan species. This was perhaps predictable, at least for some of the features, from a comparison between the regions of the seasonal changes in climate.

At Mt. Glorious there was a definite seasonal variation in temperature (Fig. 2) though winters were relatively mild. Occasional light frosts did occur in open areas, but in the forest the temperature never dropped below 4°C. There was a definite dry season which occurred in the winter, and sometimes became extended as in 1965 and 1966 (Fig. 2), but these were exceptional years. The normal pattern is for wet summers and dry winters (Kendrew, 1937). In England, although the winters are comparatively mild compared with a continental climate, they are considerably more severe than at Mt. Glorious; frosts and snow are not uncommon. Also rainfall is spread comparatively evenly throughout the year (Kendrew, 1937). In Malaya there is little seasonal variation in

temperature and rainfall, almost "to the point of monotony" (Harrison, 1952, p. 109). Thus with regard to climate, the Mt. Glorious area can be regarded as intermediate between England and Malaya.

Breeding at Mt. Glorious was seasonal, though in the two rodent species the length of the season varied considerably, and occasional pregnant or lactating animals were caught in every month of the year. In small mammals of English woodland breeding is also seasonal, (e.g. Apodemus sylvaticus and Clethrionomys glareolus, Jewell 1966a: and Sorex araneus, Shillito 1963a), and considerable variation in the length of the breeding season sometimes occurs between years in A. sylvaticus and C. glareolus (Newson, 1963; Smyth, 1966). In the Malayan rainforest no breeding season occurred in any of the nine species of rats and three species of small insectivores studied by Harrison (1955).

The pattern of growth of individuals, in the species at Mt. Glorious, showed a lull in body weight increase during the winter months. In the spring further growth took place until the mature body weight was reached. In England small woodland mammals have a similar pattern of growth e.g. C. glareolus (Jewell, 1966a), and S. araneus (Shillito, 1963a). On the other hand in Malaya small mammals grow more or less continuously to adult size (Harrison, 1956; Rudd, 1965).

The movement patterns of R. fuscipes and A. stuartii showed smaller movements for females compared with males, and female movements did not vary greatly with the seasons. The more extensive movements made by the males were particularly marked during the breeding season. In M. cervinipes however male movements were not much greater than those of females, on the average. Larger male than female movements, particularly

in the breeding season occur, in small mammals in England - A. sylvaticus (Miller, 1958), C. glareoulus (Kikkawa, 1964), and S. araneus (Shillito, 1963b). Though movement patterns of Malayan rats were not given by Harrison (1958), he noted that there was no difference in the home range size of males and females in the seven species which he studied.

At Mt. Glorious the mortality rate in sub-adult and adult R. fuscipes was comparatively constant, though during occasional short periods during the year there was a marked increase in mortality. In juveniles mortality varied considerably. In A. stuartii mortality rates were more variable. The only English woodland species for which comparative data could be found was C. glareolus. In this species mortality rates for the whole population varied considerably from one calendar period to another (Newson, 1963), and division of the population into adults and young animals showed that the lower survival rates affected not only the young animals, but also to a lesser extent the adults.

For several rats and a tree mouse in Malaya, Harrison (1956) concluded that the mortality rates were approximately constant, whatever the age or period of the year.

The fluctuations in size of the populations at Mt. Glorious varied with the species. At no time during the study did the R. fuscipes and M. cervinipes populations have peak numbers which were much more than double the minimum numbers recorded for each species (allowing that the low numbers of M. cervinipes recorded early in the study resulted from poor trappability). In A. stuartii the fluctuations were greater, the highest number recorded on the grid being seven times the minimum numbers recorded. These large fluctuations were mainly due to the unique biology of the males of this species. Populations of woodland small

mammals in England show marked fluctuations. Newson (1963) recorded peak numbers of Clethrionomys glareolus nine to twelve times the minimum numbers recorded the previous year. Kikkawa (1964) recorded a difference of nine to ten fold between the maximum and minimum numbers of Apodemus sylvaticus on his study area. Sorex araneus also show marked population fluctuations. Southern (1964) gave a peak index of population size of about 60 captures in 468 trap nights, compared with a minimum of two in 468 trap nights, on 250 acres (100 ha) of woodland during a four year study. However, for rodent species in Malaya, Harrison (1956) made the general comment that they maintained relatively stable population levels.

Two of the three species at Mt. Glorious (M. cervinipes and A. stuartii) were markedly arboreal or scansorial. Small woodland mammals in England, on the other hand, are all terrestrial (if the squirrel is not considered a small mammal.). In Malaya however (excluding squirrels, civets, etc.) three out of eleven species of shrew and five out of thirteen species of rats are arboreal or scansorial (Harrison, 1962b).

Thus the breeding, growth, and movement patterns of the three small mammals at Mt. Glorious closely resembled those of small mammals inhabiting English woodland. Their mortality rates and population fluctuations appeared to be intermediate between those of English and Malayan species, but with regard to the use they made of the vertical component of the habitat, the Mt. Glorious species resembled those in Malaya.

With respect to the breeding seasons and growth patterns of the Mt. Glorious species, their similarity to the English species could be attributed to the seasonal nature of the climate in both places, and their dissimilarity to Malayan species, to the contrasting non-seasonal

climate of Malaya. The seasonal climate at Mt. Glorious and in England generally results in a seasonal abundance in the food supply, and breeding and growth are geared to this. In Malaya the food supply is more or less constant throughout the year (Harrison 1962b), so that breeding and growth are not inhibited at any time. Insufficient is known about the factors influencing changes in mortality rates and population fluctuations to discuss the comparisons made above, with respect to these features.

The marked degree of arboreal/scansorial activity in two of the three species at Mt. Glorious, and in eight of the twenty-four comparable Malayan species, in comparison with the absence of such activity in the English species, is almost certainly due to the general similarity of subtropical rainforest to tropical rainforest, and the vast difference of both from English woodland. The lianas, creepers, and epiphytes in the rainforests provide a food source, either directly of themselves, or by virtue of the insects living in their shelter, which encourages arboreal or scansorial activity. This food source is absent in English woodland. On the other hand the dense ground layer vegetation in English woodland, which is more or less absent in rainforest, similarly provides a food source which encourages terrestrial activity.

XII SUMMARY

1. A live trapping programme was carried out in subtropical rainforest in southeast Queensland to study the three small mammals - Rattus fuscipes Melomys cervinipes (Muridae), and Antechinus stuartii (Dasyuridae).

2. Regular two weekly and later weekly trapping was carried out from September 1963 to April 1966 on a grid covering two acres (0.8 ha) to study the breeding season, growth, movements, mortality, and population size and structure. Trap lines radiating from the grid were operated at monthly intervals during one year to study dispersal movements. Monthly trapping on selected trees was carried out during another year to study arboreal activity. Three periods of continuous trapping for 24 hours were carried out in March, June, September and December 1966 to study the periodicity of activity.

3. Breeding was seasonal in all three species. In the two murids the length of the breeding season varied from year to year, but A. stuartii showed a remarkably constant breeding season. Shortly after mating male A. stuartii died. The combined pattern of breeding of the three species is discussed.

4. It was concluded from a laboratory experiment that some form of stress mechanism operated during the mating season in the males of A. stuartii causing their death. The evolution of such a mechanism is discussed.

5. Growth in R. fuscipes and A. stuartii ceased during the winter season. Body weight was found to be a suitable criterion on which to divide the R. fuscipes population into juvenile, sub-adult and adult categories. The pattern of growth was compared with the results of other workers on R. fuscipes and A. stuartii, and with other small mammals.

6. All three species occupied home ranges. In R. fuscipes and A. stuartii male home ranges and movement patterns were larger than those of females. In M. cervinipes the difference between the sexes in the size of their home ranges was much less marked. R. fuscipes had the largest home ranges, M. cervinipes the smallest. The significance of these differences is discussed in relation to body size, feeding habits and degree of arboreal activity shown by each species. Few dispersal movements were recorded in A. stuartii and juveniles of R. fuscipes, but adults of R. fuscipes made dispersal movements. None were recorded for M. cervinipes.

7. Mortality rates were investigated and compared with other small mammals. R. fuscipes mortality was relatively constant, except for juveniles, in which age group it varied considerably between calendar periods. Mortality in A. stuartii was more variable than in R. fuscipes, and the younger animals showed the greatest variability, except for the 100% mortality in males after mating.

8. Population size in R. fuscipes and M. cervinipes showed only small fluctuations, but in A. stuartii greater fluctuations occurred during the study period. This was mainly due to changes in the movement pattern, and the unique mortality pattern in the males of A. stuartii. Population structure is discussed with respect to changes in mortality rates, the number of transients, age groups and sex ratio.

9. Activity in R. fuscipes and M. cervinipes was confined to the hours

of darkness. R. fuscipes showed constant activity throughout the night. A. stuartii was partly diurnal and showed a peak of activity at dusk, and sometimes also at dawn. The results are discussed in relation to a general theory of periodicity in small mammals.

10. R. fuscipes showed practically no arboreal activity, but M. cervinipes and A. stuartii were strongly arboreal and scansorial respectively. M. cervinipes showed a preference for small trees and creeper covered trees. A. stuartii showed no preferences between tree types. The biological significance of these differences is discussed.

11. General biological features in each species are discussed in comparison with small mammals in English woodland and in Malayan rainforest. Similarities with species in English woodland were apparent.

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APPENDIX 1 The number of R. fuscipes examined each month and their reproductive condition. (PL = pregnant or lactating, NP = not pregnant, S = testes scrotal, A = testes abdominal). Figures in brackets refer to "line trapping" data.

		Female								Male					
		Adult				Sub-adult				Adult				Sub-adult	
		PL		NP		PL		NP		S		A		S	A
1963	Sept.	0		8		0		2		6		0		0	0
	Oct.	0		10		0		0		5		0		0	0
	Nov.	3		4		0		0		11		0		0	0
	Dec.	5		1		0		0		13		0		0	0
1964	Jan.	-		-		-		-		-		-		-	-
	Feb.	5		0		0		4		7		0		0	4
	Mar.	3		1		0		5		7		1		1	5
	Apr.	2		1		2		8		8		0		1	7
	May	0		4		2		7		10		0		1	5
	June	0		1		1		13		4		0		2	9
	July	0		0		0		10		4		0		2	7
	Aug.	0		4		0		5		7		0		3	2
	Sept.	1		7		0		2		14		0		1	0
	Oct.	1		7		0		1		14		0		0	0
	Nov.	3		6		0		0		12		0		0	1
	Dec.	9		0		0		1		9		0		0	2
1965	Jan.	10		1		0		1		9		0		0	6
	Feb.	5		4		0		8		10		0		0	13
	Mar.	5	(3)	4	(3)	0	(0)	10	(0)	9	(10)	0	(0)	0	(0)	16	(5)
	Apr.	6	(6)	5	(2)	1	(1)	6	(7)	8	(9)	0	(1)	0	(0)	12	(9)
	May	6	(5)	2	(4)	3	(4)	11	(10)	6	(14)	0	(1)	3	(2)	12	(8)
	June	2	(2)	7	(6)	1	(3)	10	(14)	5	(15)	0	(2)	3	(2)	9	(11)
	July	0	(1)	11	(7)	0	(0)	11	(14)	4	(7)	1	(4)	3	(2)	9	(11)
	Aug.	0	(0)	7	(14)	0	(0)	7	(16)	5	(7)	1	(0)	3	(4)	6	(10)
	Sept.	0	(0)	12	(25)	0	(0)	2	(4)	8	(24)	1	(3)	5	(5)	1	(3)
	Oct.	0	(1)	12	(22)	0	(0)	1	(2)	16	(31)	0	(0)	1	(2)	0	(1)
	Nov.	1	(5)	13	(20)	0	(0)	0	(0)	18	(29)	0	(0)	0	(0)	0	(0)
	Dec.	12	(26)	3	(5)	0	(0)	0	(0)	18	(32)	0	(0)	0	(0)	0	(0)
1966	Jan.	10	(11)	3	(13)	0	(0)	3	(4)	12	(20)	0	(0)	0	(0)	6	(2)
	Feb.	2	(1)	5	(19)	0	(0)	4	(5)	5	(16)	0	(1)	0	(0)	3	(4)
	Mar.	1		6		0		4		6		0		0	2
	Apr.	1		6		0		4		3		0		0	2
	June	0		6		0		4		0		3		0	1
	Sept.	2		6		0		0		8		0		0	0
	Dec.	5		0		0		1		10		0		0	1

APPENDIX 2 The number of M. cervinipes examined each month and their reproductive condition.
(PL = pregnant or lactating, NP = not pregnant, S = testes scrotal, A = testes abdominal).
"Grid" and "line trapping" data combined.

		Female				Male			
		Adult		Sub-adult		Adult		Sub-adult	
		PL	NP	PL	NP	S	A	S	A
1963	Sept.	0	2			0	0	0	0
	Oct.	0	3			0	0	0	0
	Nov.	2	1			1	0	0	0
	Dec.	0	0			1	0	0	0
1964	Jan.	-	-	-	-	-	-	-	-
	Feb.	1	1			0	0	0	1
	Mar.	0	0			0	0	0	0
	Apr.	0	0	0	1	0	0	0	1
	May	0	1	0	3	0	0	0	0
	June	0	1	0	3	0	0	1	3
	July	0	1	0	3	1	0	2	2
	Aug.	0	4	0	3	4	0	5	1
	Sept.	2	6	0	0	6	0	0	0
	Oct.	5	6	0	0	6	0	0	0
	Nov.	1	1	0	2	3	0	0	0
	Dec.	2	2	0	3	1	0	0	1
1965	Jan.	1	2	0	2	1	0	0	1
	Feb.	2	1	2	3	1	0	0	2
	Mar.	2	0	3	0	3	1	0	2
	Apr.	2	0	1	2	5	3	0	2
	May	0	0	2	2	2	0	0	3
	June	2	1	1	5	1	0	0	4
	July	1	4	0	2	3	0	1	2
	Aug.	0	2	0	6	4	0	3	2
	Sept.	6	8	0	0	15	0	0	0
	Oct.	11	2	0	0	9	0	0	0
	Nov.	8	2	0	0	9	1	0	1
	Dec.	6	2	0	0	2	0	0	1
1966	Jan.	2	3	0	1	0	1	0	1
	Feb.	1	4	0	0	1	0	0	0
	Mar.	0	4	0	3	3	2	0	0
	Apr.	0	3	0	3	0	1	0	1
	June	0	3	0	2	6	3	0	2
	Sept.	1	7	0	0	11	0	0	0
	Dec.	3	1	0	0	1	0	0	0

APPENDIX 3 Reproductive states of *A. stuartii* ♀♀.
(Total number of individuals captured at least once in this analysis = 82).

	October				November				December				January				February			
Weeks	1	2	3	4+	1	2	3	4+	1	2	3	4+	1	2	3	4+	1	2	3	4
63/64																				
Total ♀ catch		9		9		9		8	3	5	5					5		5		4
females carrying young		0		9		9		7⊕	0	0	0					0		0		0
females lactating		0		0		0		0	3	5	5					5		4		3
64/65																				
Total ♀ catch	11		8	9	7	11		9		8		10	7		10	14	15	7	9	8
females carrying young	0		0	9	7	11		7		0		0	0		0	0	0	0	0	0
females lactating	0		0	0	0	0		2*		8		9⊕	7		10	14	14⊕	7	7	7
65/66																				
Total ♀ catch	22	5	5	20	3	5	7	11	2	2	16	11	2	3	19	3	4	4	2	9
females carrying young	0	0	2*	17**	3	5	7	11	0	0	0	0	0	0	0	0	0	0	0	0
females lactating	0	0	0	0	0	0	0	0	2	2	14⊕	10⊕	2	3	17⊕	3	4	3	1⊕	8
1963 - 66																				
Total ♀ catch	33	14	13	38	10	25	7	28	5	15	21	21	9	3	29	22	19	16	11	21
females carrying young			2	35	10	25	7	25	0											
females lactating								2	5	15	19	19	9	3	27	22	18	14	8	18
reproduction failures***				1				1			2	2			2		1	0	1	0

*** Recaptures of animals which failed to reproduce not recorded in this table so total failures = 10.
** Only 1 reproduction failure here.
* Both on last day of period.
⊕ Reproduction failure.

Appendix 4 Values of C_0, C_1 and S_1 from which R. fuscipes population estimates in Appendix 5 were calculated.

	C_0	C_1	S_1
1963			
September	2	16	2
October	14	13	10
November	14	16	12
December	17	15	13
1964			
January			
February	13	16	10
March	18	18	14
April			
May	23	16	11
June	22	24	18
July	17	13	11
August	12	19	12
September	18	16	12
October	20	16	15
November	14	16	11
December	13	18	10
1965			
January	18	23	13
February	27	30	19
March	28	28	18
April	27	29	18
May	28	27	20
June	21	20	15
July	24	23	20
August	21	22	16
September	25	24	21
October	23	23	19
November	20	20	11
December	19	27	17
1966			
January	23	23	15
February	14	12	11
March	19	18	18
April	12	12	8
June	12	17	12
September	9	16	9
December	10	12	6

Appendix 5 Population estimates of R. fuscipes.

$$N^1 = \frac{C_0.(C_1 + 1)}{(S_1 + 1)} \qquad V(N^1) = \frac{(N^1)^2.(C_1 - S_1)}{(C_1 + 1)(S_{1+2})}$$

N^2 = Number of animals known to be alive. $S.D.(N^1) = \sqrt{V(N^1)}$

	N^2	N^1	$S.D.(N^1)$
1963			
September	16	11.3	5.12
October	17	17.8	2.38
November	18	18.3	2.37
December	19	19.4	2.80
1964			
January	-	-	
February	19	20.0	1.60
March	24	22.8	2.62
April	-	-	
May	30	32.6	4.90
June	29	28.9	3.17
July	22	19.8	2.08
August	21	18.5	2.92
September	22	23.5	3.05
October	21	21.2	2.50
November	20	19.8	2.98
December	21	22.4	4.20
1965			
January	28	30.8	5.14
February	41	41.8	5.44
March	41	42.7	5.61
April	40	42.6	5.76
May	39	37.3	3.91
June	34	27.6	3.26
July	31	27.4	2.34
August	26	28.4	3.42
September	28	28.4	2.70
October	27	27.6	2.45
November	31	23.3	4.23
December	32	29.5	4.05
1966			
January	33	34.5	4.83
February	18	15.1	1.15
March	21	19.0	0.00
April	19	17.3	3.04
June	18	16.6	2.33
September	16	16.7	3.22
December	17	18.6	4.47

Appendix 6 Values of C_0, C_1 and S_1 from which *M. cervinipes* population estimates in Appendix 7 were calculated.

	C_0	C_1	S_1
1963			
September	0	2	0
October	2	2	1
November	3	1	0
December	1	0	0
1964			
January			
February	1	2	0
March	0	0	0
April			
May	2	4	1
June	3	4	0
July	7	5	3
August	6	11	2
September	8	10	4
October	16	8	6
November	4	4	1
December	3	1	0
1965			
January	6	6	3
February	5	5	1
March	9	4	2
April	3	2	1
May	5	8	3
June	10	6	5
July	8	2	0
August	13	11	10
September	14	16	9
October	14	10	9
November	8	15	5
December	3	3	1
1966			
January	5	3	2
February	3	0	0
March	3	8	2
April	4	5	1
June	7	8	3
September	5	12	4
December	2	1	0

Appendix 7 Population estimates of *M. cervinipes*.
For symbols N^1, N^2 and S.D.(N^1) see Appendix 5

	N^2	N^1	S.D.(N^1)
1963			
September	2	-	
October	3	-	
November	4	-	
December	1	-	
1964			
January	-	-	
February	3	-	
March	2	-	
April	-	-	
May	6	5.0	2.23
June	7	15.0	9.49
July	9	10.5	2.97
August	16	24.0	3.30
September	16	17.6	5.31
October	18	20.5	3.42
November	11	10.0	4.48
December	10	6.0	3.00
1965			
January	14	10.5	3.08
February	15	15.0	7.07
March	16	22.5	7.08
April	12	4.5	1.50
May	17	11.2	3.73
June	21	14.0	2.00
July	23	24.0	13.85
August	25	14.1	1.18
September	26	23.8	4.60
October	21	15.4	1.40
November	20	21.2	6.33
December	12	6.0	2.45
1966			
January	13	6.6	1.66
February	10	3.0	0.00
March	15	9.0	3.67
April	14	12.0	5.65
June	18	15.7	5.23
September	18	13.0	4.16
December	4	4.0	2.00

Appendix 8 Values of C_0, C_1 and S_1 from which *A. stuartii* population estimates in Appendix 9 were calculated.

	C_0	C_1	S_1
1963			
September	8	19	1
October	9	9	7
November	9	8	7
December	6	5	4
1964			
January			
February	8	14	5
March	10	12	4
April			
May	23	14	10
June	38	33	26
July	28	29	25
August	23	21	18
September	33	33	22
October	12	10	8
November	11	8	7
December	8	10	8
1965			
January	8	14	7
February	19	28	14
March	28	21	17
April	21	20	17
May	26	28	23
June	29	18	14
July	24	12	11
August	11	11	9
September	10	9	6
October	5	8	4
November	7	4	4
December	3	5	2
1966			
January	4	5	3
February	7	4	3
March	19	15	14
April	16	14	10
June	24	30	20
September	13	17	11
December	5	4	4

Appendix 9 Population estimates of *A. stuartii*.
For symbols N^1, N^2, S.D.(N^1) see Appendix 5.

	N^2	N^1	S.D.(N^1)
1963			
September	29	80.0	43.82
October	12	11.2	1.67
November	11	11.5	1.27
December	7	7.0	2.60
1964			
January	-	-	
February	18	20.0	5.85
March	23	26.0	8.32
April			
May	34	31.3	4.66
June	48	47.8	4.10
July	39	32.3	2.27
August	36	26.6	2.19
September	46	48.7	5.65
October	19	14.6	1.96
November	17	12.3	1.36
December	14	9.7	1.30
1965			
January	18	15.0	3.42
February	36	36.6	6.35
March	35	34.2	3.34
April	32	24.5	2.12
May	35	31.4	2.56
June	33	36.9	4.21
July	28	26.0	2.00
August	17	13.2	1.63
September	16	14.2	2.75
October	9	9.0	2.45
November	10	7.0	0.00
December	9	6.0	2.12
1966			
January	8	6.0	1.55
February	10	8.7	1.74
March	20	20.2	1.26
April	24	21.8	3.25
June	34	35.4	4.28
September	19	19.5	3.60
December	5	5.0	0.00


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